THE FAUNA AND PALEOECOLOGY OF THE LATE MIOCENE MOSS ACRES RACETRACK SITE, MARION COUNTY, FLORIDA

by

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LIST OF COLLECTION ABBREVIATIONS

(OTHER ABBREVIATIONS EXPLAINED IN THE TEXT)

D.M.N.H.: Denver Museum of Natural History, Denver, Colorado

K.U.M.: University of Kansas, Lawrence, Kansas

MCZ: Museum of Comparative Zoology, Cambridge, Massachusetts

T.M.M.: Texas Memorial Museum, Austin, Texas

UF: Florida Museum of Natural History Collection of Paleontology, Gainesville, Florida

UF(M): Florida Museum of Natural History Collection of Mammalogy, Gainesville, Florida

UM-V: University of Michigan Vertebrate Paleontology Collection, Ann Arbor, Michigan

UNSM: Nebraska State Museum, Lincoln, Nebraska

USNM(M): Smithsonian Institution Mammalogy Collection, Washington D.C.

Abstract of Dissertation Presented to the Graduate School of
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THE FAUNA AND PALEOECOLOGY OF THE LATE MIOCENE MOSS ACRES RACETRACK SITE, MARION COUNTY, FLORIDA

By

W. David Lambert

April, 1994

Chairman: Dr. S. David Webb
Major Department: Zoology

The Moss Acres Racetrack site represents an early Hemphillian age, clay-filled sinkhole in western Marion County, Florida,with a diverse biota, possibly containing more evidence for local biotic and climatic conditions than any other late Miocene locality on the Gulf Coastal Plain. The geology, taphonomy, fauna, palynoflora, and community ecology of this locality were all examined in this study.

Geological and taphonomic evidence suggests that the fossil biota was preserved under strictly nonfluvial conditions in an isolated pond or lake, indicating that this assemblage represents a real community rather than a mixed-assemblage. The faunal description included detailed study of the following mammalian taxa: the gomphothere proboscidean *Amebelodon* (*Konobelodon*) *britti* (described as a new subgenus and species), the ground sloth *Pliometanastes* (represented by previously unknown limb elements), the giant otter *Enhydritherium* (represented by a partial skeleton, the best bunodont otter specimen known), and the dromomerycid ruminant *Pediomeryx* *hemphillensis* (including a partial skull with

ly intact horn cores), and the rhinoceros *Aphelops* *ilis*. Other mammal taxa (including the horses) were mined in a cursory fashion only. Preliminary evidence gests the presence of a new species of the emydid turtle *udemys* and a new species of *Alligator* within the petofauna. The palynoflora revealed a dominance by grass oak suggesting a savanna landscape, with all other taxa ividually forming minute portions of the flora. The floral t resembles that of a modern warm temperate woodland in southeastern United States, suggesting temperatures ilar to those found in the region today. Rainfall patterns inconclusive, though the presence of a savanna landscape ggests strong seasonal aridity.

The nature of community interactions within the biota largely inconclusive. Terrestrial carnivores were tually absent, possibly a result of small sample size. dence for facilitative grazing like that found in modern ican savannas was searched for, with the final results ing ambiguous. *Amebelodon* was shown to be a plausible logical analog for modern African elephants in savannas, earing woodlands to limit their spread into the grasslands thus encouraging and maintaining biotic diversity.

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CHAPTER 1
INTRODUCTION

The Moss Acres Racetrack site consists of a sinkhole within both Eocene and Miocene limestone in Marion County, Florida, near the small town of Morriston in Levy County (map coordinates NW 1/4, NE 1/4 sec. 11, T14S, R19E, Morriston Quad.) (Figure 1-1). The site was initially discovered in 1984, when during construction of a racetrack fossils were discovered on the Moss Acres South horse farm. John Shimfessel, the owner of the site, brought this discovery to the attention of the Florida Museum of Natural History and generously gave permission for the site to be worked when its importance was revealed. Museum crews worked Moss Acres Racetrack and made an extensive collection of specimens until spring of 1987, at which point the site was closed. Though small amounts of material was collected in the summer of 1989, work at Moss Acres Racetrack did not restart in significant degree until April of 1991. The site was only worked until the middle of June of that year, though during this brief period the collection of Moss Acres Racetrack material was enriched considerably including the recovery of some spectacular specimens. The site has not been worked professionally since.

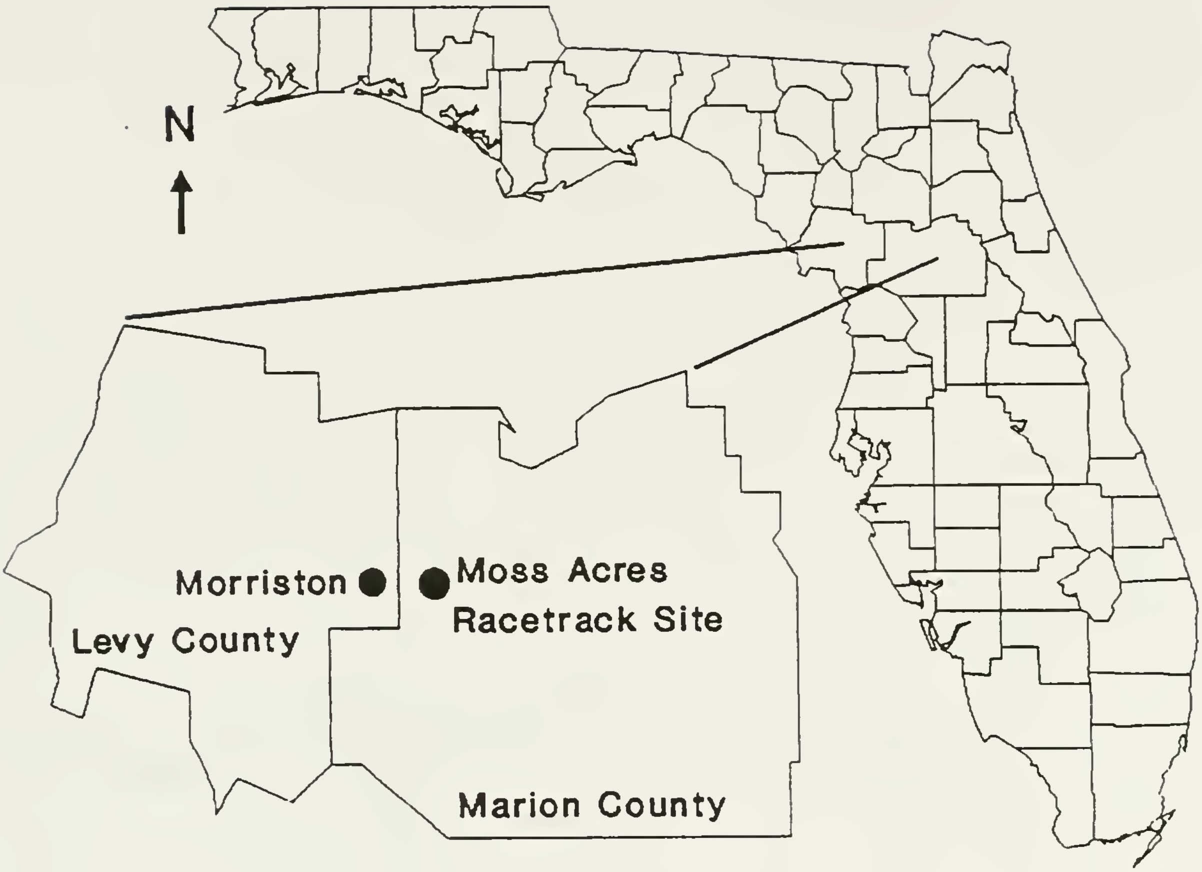


Figure 1-1. Map of Florida showing the location of the Moss Acres Racetrack locality.

The Moss Acres Racetrack fauna is remarkable primarily for three reasons: the overall high quality of specimen preservation, the preservational circunmstances of the specimens, and unusual ecological biases in the animals represented. Many of the specimens preserved are partial associated and even articulated skeletons, a rare occurrence in Florida, and the fauna evidently represents an unmixed local community in the sense that there is no evidence that any of the specimens were transported by water from other localities and mixed with the remains of animals that actually died at the site. The site has yielded a fauna of large herbivores dominated by hooved mammals, the most impressive of which is the shovel-tusked gomphothere *Amebelodon* for which this is one of the richest localities in the world. Other herbivores found at the site include the giant ground sloth *Pliometanastes* (a possible ancestor of *Megalonyx*), a wide variety of horses including both tridactyl and monodactyl taxa, the rhinoceros *Aphelops*, an unidentified peccary, two camels (one a long-necked giant, and the other comparable to a modern lama), the hornless deer-like ruminant *Pseudoceras*, and the strange horned ruminant *Pedomeryx*, which has a single horn protruding out the back of its head as well as two ordinary frontal horns. However, surprisingly despite the abundance of herbivores terrestrial carnivores are virtually absent from the fauna, the only confirmed representative being the small "bone-eating" dog *Osteoborus orc* known on the basis of a few isolated specimens. Aquatic carnivores at the site include an abundance of alligators and a single partial skeleton of the giant otter *Enhydritherium* (possibly related to the living sea otter), the most complete specimen of a fossil "bunodont" otter known in the world.

The Moss Acres Racetrack fauna is clearly exceptional in terms of its faunal richness. However, this faunal richness by itself does not give this site special paleontological significance, many sites close in age being equally rich or richer (e.g., the Coffee Ranch, Texas [Schultz, 1977]; Rhino Hill, Kansas [Bennett, 1977]; and the Love Bone Bed, Florida [Webb *et al.*, 1981]). Rather, the importance of this site stems principally from three factors: 1) unique specimens known from the fauna (including the well preserved skulls of the famous genus *Amebelodon*, an element unknown from any other site in the world; a nearly complete skeleton of the "bunodont" otter *Enhydritherium*, the most complete specimen in the world for this type of otter; the associated fore- and hindlimbs of the ground sloth *Pliometanastes*, preserving elements previously unknown for this genus; and the first *Pediomeryx* skull ever found, even preserving intact the occipital and frontal horns); 2) despite ecological biases, the nearly complete preservation of one aspect of the fauna, the ungulate "community;" and 3) a well preserved palynoflora, a rarity in Tertiary sites of southeastern North America, particularly in association with a good terrestrial vertebrate fauna. Despite these factors, the Moss Acres Racetrack fauna as a whole is largely unstudied. The only taxonomic group in the fauna examined in detail is the horses (Hulbert, 1987; 1988a; 1988c; 1993b), with the other portions of the fauna remaining undescribed. Lacking a proper taxonomic description, it has remained impossible to perform a proper paleoecological analysis of the locality including a comprehensive examination of the climate, flora, and fauna, an analysis that can be performed on very few localities because of such limitations as faunal gaps and an unknown flora. Indeed, no such late Miocene localities have been studied from the southeastern United States at all, with a result that little is known about the ecological conditions in this region during this time.

The goal of this dissertation is a complete taxonomic description of the Moss Acres Racetrack fauna, going beyond the the work done by Hulbert on the horses, and the utilization of this description in combination with other data to create a paleoecological reconstruction of the locality. The first chapter of this dissertation will examine the geology at the Moss Acres Racetrack site, providing insight into the physical habitat in which the fossil community existed. Subsequent chapters will focus on describing the fauna, with an emphasis placed on osteological description but with systematics (including phylogeny) and autecology also addressed where appropriate. Since they comprise the majority of the fauna in terms of diversity and abundance, and have the potential to provide the most ecological information, mammals are emphasized over the reptiles in this description (birds, amphibians, and fish being largely or completely unknown for unexplained reasons), though reptiles are addressed. Following the taxonomic descriptions is a chapter on the taphonomy of the Moss Acres Racetrack, combining geological with taxonomic information to investigate the conditions that led to the fossil preservation of the fauna. Finally, all of the geological, faunal, and taphonomic information from the preceding chapters are combined in an analysis of the paleoecology of the Moss Acres Racetrack site, examining the paleoclimate and possible community interrelationships (including plant-animal and animal-animal) that existed originally at the locality. This analysis provides new information about the poorly known ecological conditions that existed in the southeastern United States (and to an extent North America as a whole) during the late Miocene and some of the key factors that may have influenced them.

CHAPTER 2
THE GEOLOGY AND AGE OF THE MOSS ACRES RACETRACK SITE

Geology

The Moss Acres Racetrack site consists of a clay bed of unknown depth and extent, containing limestone fragments and having at least a small, local floor of sandy, phosphatic limestone. The stratigraphy is only known from a single exposure, the majority of fossils recovered from horizontally oriented exposures from which stratigraphy could not be discerned. Although bones have been recovered from all but the most superficial levels of the clay bed, the vast majority have come from from a single unit approximately one meter thick. The regional stratigraphic relationships and local sedimentary facies shed light on both the nature of the preservation of fossils at the site and the ecology of the preserved paleocommunity as a whole.

Regional Geology

The most prominent geological units in northcentral Florida are the Ocala Limestone (a group including three formations, the Inglis, Williston, and Crystal River), the Hawthorn (variably called both a formation and a group; see below), and the Alachua Formation (a lithologically diverse unit of uncertain stratigraphic relationship to the aforementioned units) (Vernon, 1951; Scott, 1988; and Puri and Vernon, 1964), and these formations are most relevant to the Moss Acres Racetrack site. Other units variably present in northcentral Florida, including the Suwannee (limestone) and Citronelle Formations (Vernon, 1951; Scott, 1988; and Pirkle et al., 1965), have no bearing on the site and are not discussed further here.

In northcentral Florida the Eocene Ocala Limestone forms an effective basement on which all younger sediments are superposed. Over much of northcentral Florida, as in the state as a whole, sediments tend to overlay the Ocala Limestone in a fairly ordinary (if unconformable) fashion, the superpositioned units being level relative to each other (with one exception being localized karst infillings; see below). The Ocala is a relatively uniform unit lithologically, composed of an essentially pure marine biogenic limestone with clastics nearly or completely absent. In regions of Levy, Marion, Alachua, and Citrus Counties the Ocala Limestone rises locally to form a single, distinctly ridge-like structure commonly called the Ocala Arch; sediments along the slopes of this structure form a skin that gradually decreases in thickness with rising elevation, vanishing near the top of the arch to leave the Ocala Limestone largely exposed (Puri and Vernon, 1964; Vernon, 1951). Most of the karst activity in northcentral Florida involves dissolution of basement Ocala limestone rather than overlying limestones such as the Hawthorn, Hawthorn karst formation being more typical of the southern half of Florida (Puri and Vernon, 1964; see below).

The majority of the Neogene sediment covering the Ocala limestone in northcentral Florida consists of the Hawthorn (Scott, 1988). Traditionally, the Hawthorn has been treated in the literature as a single formation (e.g. Pirkle, 1956; Puri and Vernon, 1964). However, Scott (1988) promoted the Hawthorn to the status of a group, establishing within it a number of new formations that vary between the northern and the southern halves of the peninsula. In northcentral Florida new formations established within the Hawthorn by Scott (1988) include in order from bottom to top: the Penney Farms, Marks Head, and Coosawhatchee Formations, with the Statenville Formation encompassed by the Coosawhatchee. The question of whether the Hawthorn is properly a formation or a distinct group is an issue beyond the scope and intent of this study, and henceforth the Hawthorn will be referred to without specific reference to its unit status. The Hawthorn is an extremely heterogeneous unit lithologically, consisting of clays, sands, dolomites, and limestones (both calcitic and dolomitic), with phosphate nodules (phosphorite) present throughout. In some localities, extensive phosphate concentrations occur in the main body of the Hawthorn; these accumulations consist of pebbles and grains of phosphorite embedded in a matrix that may be all quartz sand, clay, or carbonate, but usually is a mixture of these sediments (Pirkle et al., 1965). The Hawthorn represents a marine and/or estuarine facies, as indicated by its mollusk fauna and the abundance of phosphorite (Scott, 1988; Vernon, 1951; and Pirkle, 1956)

The Alachua Formation is a controversial unit, considered to be a true formation by some (e.g., Sellards, 1914; Vernon, 1951; and Puri and Vernon, 1964), and a unit of uncertain status, possibly not a true formation at all (e.g., Scott, 1988). The uncertainty about the formation status of the Alachua Formation stems from two factors: 1) a discontinuous geographical distribution with an associated ambiguity as to stratigraphic relationship to adjacent units; and 2) a complex, highly variable lithology.

Alachua sediments are not continuous, but rather form distinct pockets in localized limestone basins scattered throughout northcentral Florida (it is found in two distinct zones separated by a gap, Gilchrest, Levy, Alachua, and Marion Counties to the north and Citrus, Sumter, and Pasco Counties to the south [Brooks, 1981]). Thus, unlike a proper formation it is neither traceable nor mappable. In addition, Alachua sediments cannot be clearly placed into a stratigraphic sequence relative to neighboring formations. Alachua Formation sediments are known in pockets of the Ocala Limestone (particularly near the top of the Ocala Arch), the Suwannee, and Hawthorn limestones. Thus considering that the rules of the North American Stratigraphic Code require a formation to be mappable and have a distinct stratigraphic position (Boggs, 1987), it is difficult to justify calling the Alachua a true formation.

It is difficult to characterize the lithology of the Alachua Formation because of its variability. However, it can be crudely described as a terrestrial, lacustrine, and/or fluviatile mixture of interbedded, irregular deposits of clays, sand, and sandy clay of diverse characteristics. Though considerable variation exists, the Alachua Formation typically has the following stratigraphy. The upper portion is characterized by faintly stratified, cross-bedded, poorly indurated, fine-grained gray quartz sand contained in a matrix of unidentified phosphatic clay mineral. Interbedded with and commonly underlying these sands are occasional pebbles of waterworn flint, erratic boulders of limestone, silicified limestone and flint, clay lenses, pebbles, and boulders of phosphorite, phosphatic clay conglomerate, colloidal phosphate, and an occasional concentration of vertebrate fossils. The abovementioned clay lenses are formed by montmorillonite in light pastel shades of green and blue, occasionally containing phosphorite (at best a minor constituent) and silicified clay. This clay is waxy, blocky, and irregular in its distribution though it commonly separates concentrations of phosphorite from underlying limestone. The floor of the Alachua Formation is formed by phosphorite rubble, silicified limestone residuum, and silicified wood contained in a matrix of cream to gray phosphatic clay and greenish-gray waxy clays (Vernon, 1951; Vernon and Puri, 1964).

Terrestrial vertebrate faunas collected from Alachua sediments range from early Miocene (e.g., the Hemingfordian Thomas Farm Local Fauna) to Pleistocene (e.g., many local faunas from the Haile complex) in age (Vernon, 1951; Puri and Vernon, 1964). Thus, these sediments have a chronological range of at least 15 million years, which could intuitively reduce the credibility of the Alachua as a formation. It should be noted, however, that neither chronological range nor continuity are crucial considerations in determining the formational status of a unit according to the North American Stratigraphic Code (Boggs, 1987).

Stratigraphy of the Moss Acres Racetrack Site

Virtually all stratigraphic information on the Moss Acres Racetrack site is based on a single vertical exposure excavated when the site was worked in 1991. The clay bed of the Moss Acres Racetrack site can be divided into four distinct units numbered consecutively from top to bottom, excluding the superficial covering of grass and topsoil. Approximations of the relative thicknesses of the units along with brief descriptions are presented in Figure 2-1.

Unit 1 is a white, unconsolidated clay layer roughly 60 centimeters or less in thickness, differing from all of the other clay units at the site in possessing significant impurities of sand and small marl pebbles, perhaps

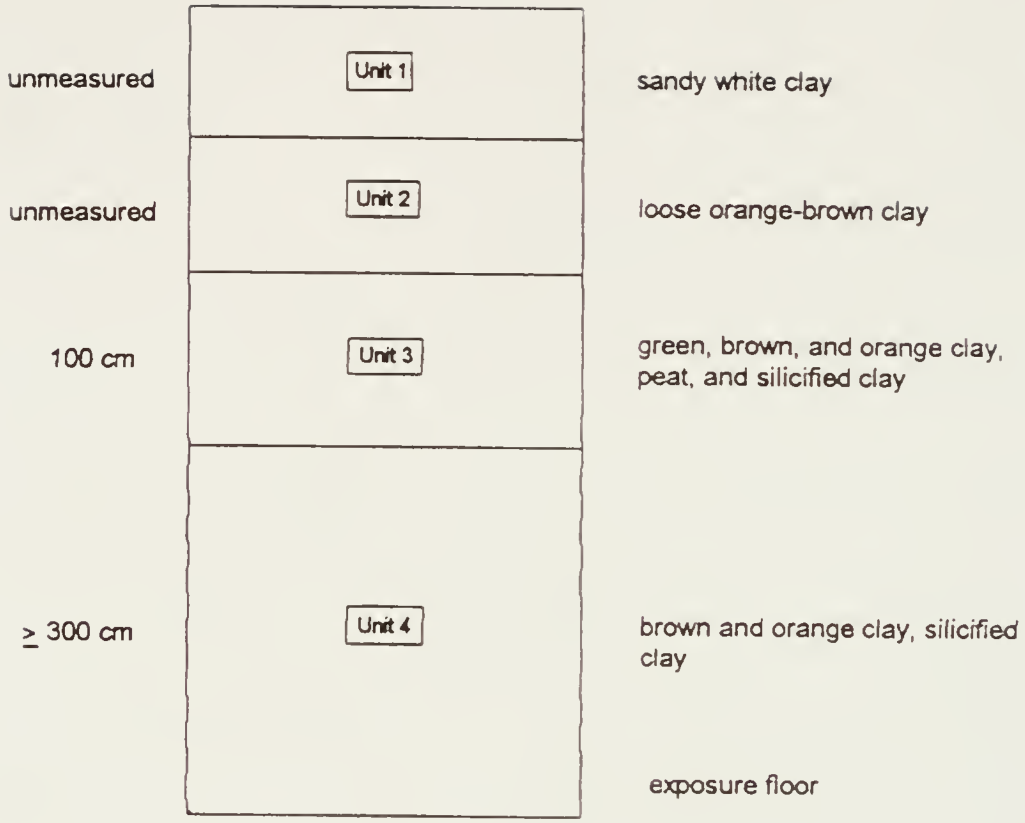


Figure 2-1. Schematic diagram illustrating the sedimentological stratigraphy of one exposure at the Moss Acres Racetrack site.

deteriorated caliche nodules. No fossils, vertebrate or invertebrate, have been found in this unit.

Unit 2 clay is darker than unit 1, being orange-brown in color (possibly due to oxidation). Unlike unit 1 it is a pure clay, with no signs of sand or other impurities beyond isolated chunks of suspended limestone. Unit 2 resembles unit 1 in being poorly consolidated, possibly due to weathering. Vertebrate fossils have been recovered from unit 2, but these fossils are poorly preserved, a condition consistent with the hypothesis that this unit has been subjected to considerable weathering (see chapter 9).

Unit 3 is the most fossiliferous unit in the site. Like unit 2 the unit 3 clay appears to be quite pure. It has few impurities except for some large chunks of limestone and phosphate pebbles, presumably reworked from adjacent walls. Small amounts of fine silica sand and isolated pockets of peat also occur in Unit 3. The clay varies considerably in color, ranging from orange to brown, blue, and green; much or most of it is heavily streaked by numerous dark lines with no preferred orientation, perhaps due to some elemental contamination (similar streaks are abundant on the fossil bones taken from the site). Isolated pockets of unit 3 clay contain degraded peat, identified by L. Newsome (pers. comm.), which gives the clay a dark gray or black color and a greasy texture. When freshly exposed, the clay of this unit is distinctly blocky with a shiny, waxy appearance. When wet, the freshly exposed clay forms a stiff, viscous "sludge," on drying becoming extremely crumbly and swiftly expanding when exposed to water to form a foam. In addition to the blocky, waxy clay, there are pockets of clay with a texture reminescent of soft limestone. Such pockets presumably represent silicified clay, which is known in both the Hawthorn and the Alachua Formations (Pirkle et al., 1965; Vernon, 1951). Pockets of this hardened clay tend to be particularly abundant in this unit near accumulations of fossil bone, suggesting two possibilities: 1) local diagenetic processes involving biological material may have influenced the chemistry of the surrounding matrix; or 2) the organisms helped introduce or were accompanied by material not normally deposited in the site. While significantly thicker than units 1 and 2, unit 3 is not particularly thick as a whole, measuring approximately a meter in the measured section of the vertical exposure and probably not exceeding 1 1/2 meters anywhere in the exposure. The contact between units 3 and 2 is fairly distinct; however, in contrast the contact between units 3 and 4 is rather subtle, in part because of the strong similarity in color and superficial texture between the clays (see below).

Unit 4 is not dramatically different in appearance from unit 3. Unit 4 is typically brown and orange, unlike unit 3 which displays blue and green as well as brown and orange hues. Nevertheless Unit 4 can be distinguished from 3 by the much greater abundance of silicified clay and the complete absence of peat. Like the clay in unit 3, freshly exposed unit 4 clay is blocky and waxy when unsilicified. Vertebrate fossils are essentially absent from this unit, although one heavily worn, isolated Aphelops vertebra was encountered. Unit 4 is by far the thickest of the four units, having a minimal thickness of three meters (the depth to the floor of the deepest part of the exposure). The full thickness of this unit could not be determined, nor could the possibility of lateral variation be investigated due to the small size of the exposure.

The clay bed of Moss Acres Racetrack must contact an underlying limestone unit, but no such unit was exposed in the measured secion. An exposure of yellowish sandy limestone was observed in the infield region of the track when the site was worked between 1985 and 1987 (Webb and Morgan, pers. comm). This limestone exposure lay just north of the productive clay exposures and protruded upward into the clay, either Unit 3 or 4. This limestone contained considerable amounts of sand and water worn phosphatic gravel (Morgan, pers. comm.), and almost certainly represents Hawthorn limestone. This limestone produced a few phosphatized shark teeth, e.g., Negaprion brevirostris, Galeocerdo sp., and Carcharodon auriculatus, which help corroborate an early Miocene age. Reworked invertebrate fossils diagnostic of the Eocene have been found in the clay as well, indicating that the clay is or was at one time in contact with Ocala as well as Hawthorn limestone. However, the positional relationship of the Ocala Limestone to the clay bed and the Hawthorn is unknown.

Mineralogy

A sample of clay from unit 3 was sent to Dr. McCartan of the United States Geological Survey for mineralogical analysis by X-ray differaction. The result of this analysis is as follows. The clay is not montmorillonite, commonly attributed to some residues of the Hawthorn as well as the Alachua Formation (Vernon, 1956; Puri and Vernon, 1964), but rather is 80% illite and 20% kaolinite. The clay is remarkably pure, showing no signs of heavy minerals such as garnet, zirconium, and tourmaline, common in Hawthorn sediments including clays (Pirkle et al., 1956). Phosphates are also absent except for rare, isolated nodules probably reworked from the Hawthorn. The only significant mineralogical impurity observed is silica, present only as minute grains and perhaps formed by the precipitation of silicic acid resulting from the hydrolytic breakdown of silicate minerals (see below).

This mineralogy has strong implications for the conditions under which these sediments were formed. Both illite and kaolinite are formed by subaerial weathering. Kaolinite tends to form under severe chemical leaching conditions that cause removal of all soluble cations except silicon and aluminum. Illite forms under less severe chemical leaching conditions in a potassium-rich environment, such as when potassium feldspar-rich rocks (e.g., granites) are broken down (Boggs, 1987). The presence of the silica grains in the clay suggests the possibility that localized mineral breakdown occurred at the site. The hydrolysis of silicates that leads to the formation of clays such as kaolinite and illite also forms silicic acid (H_4SiO_4) as a by-product, which can precipitate into small grains of silica (SiO_2) as well as combine with cations to form clay (Boggs, 1987). Though not examined by X-ray analysis, the hardened clays in units 3 and unit 4 are in all likelihood silicified, conceivably through the process of percolation and precipitation of silicic acid.

Formational Status of the Moss Acres Racetrack Site

The Moss Acres Racetrack site has two major geological features, the clay bed and the underlying limestone. The limestone formation(s) have only a minor bearing on the paleoecology and taphonomy of the mammal fauna of Moss Acres Racetrack, are discussed above, and will not be further considered here. Thus, the following discussion concentrates on the clays.

The Moss Acres Racetrack clay bed can be plausibly referred to only the Hawthorn or the Alachua Formation, since of the major geological units found in northcentral Florida only these extend into the Miocene and are known to contain extensive lenses of clay or clay-dominated sediment (Vernon, 1951; Pirkle, 1956). The Hawthorn can be eliminated as a likely source of the clay on the basis of a number of factors, including: 1) the virtual absence of phosphorite from at least units 2-4 (with the condition of unit 1 currently unknown), 2) the complete absence of such heavy minerals as garnet, tourmaline, and zircon, and 3) a probable origin of the clay from a fresh water rather than a marine facies, as indicated by the presence of peat in unit 3 and the absence of a distinctive *in situ* marine fauna. The clay bed bears a distinct resemblance to the clay lenses sometimes found in the Alachua Formation, having a similar texture (e.g., a blocky, waxy appearance with some silicification), color (shades of blue and green for the Alachua clay as compared with blue, green, orange, and brown for the Moss Acres Racetrack clay in unit 3, and the blue and green in unit 4), and facies (both fresh water/terrestrial). The mineralogy appears to differ considerably between the two, the Alachua clay being composed of montmorillonite rather than the kaolinite and illite mixture found in Moss Acres Racetrack. However, the possibility exists that the presence of montmorillonite in the Alachua clay cited by Vernon (1951) was the result of a misidentification, since the illite/kaolinite mixture of Moss Acres Racetrack superficially resembles montmorillonite and no formal X-ray analysis of the Alachua Formation montmorillonite was mentioned. Thus, the Moss Acres Racetrack clay can be plausibly linked with the Alachua Formation clays as defined by Sellards (1914), Vernon (1951), Pirkle (1956), and Vernon and Puri (1964). However, the question of the validity of the Alachua Formation as a whole aside, the lithostratigraphic unity of these clay beds is doubtful. Considering that "Alachua clays" can overlie Ocala, Hawthorn, and even Suwannee limestones and the wide range in age of faunas found in these clays, it appears likely that the Alachua Formation sediments, particularly the clay lenses, are the result of a number of chronologically and geographically isolated local events rather than a single chronologically continuous, geographically wide-spread deposition event.

Origins of the Moss Acres Racetrack Site

This section addresses the question of how the sediments (specifically the clays) were laid down at the site, since their lithogenesis has relevance to the preservation of vertebrate bones. A geologist would normally study the geomorphology of surrounding sedimentary units to determine whether the sediments had been laid down on a floodplain, or else had filled a depression such as a graben, karst, or a channel such as a river bed. Unfortunately the sediments in the area of Moss Acres Racetrack are poorly exposed and not mapped geologically in any detail, so that there is virtually no direct information regarding the geomorphology of the adjoining units. Thus, inferences regarding the lithogenesis of the fossiliferous clays must be drawn from the evidence of clay mineralogy and the nature and condition of the preserved bones themselves.

The mineralogy of the Moss Acres Racetrack clays has strong implications for their origins. As discussed above these clays are nearly pure, being virtually free of contaminants such as sand and heavy minerals (excluding the minute silica grains, which were probably formed with the clay itself and therefore not a contaminant). The clays are composed of the minerals illite and kaolinite, both of which are products of the chemical breakdown of other parent minerals such as feldspar during subaerial weathering. However, it is unclear whether this process occurred immediately *in situ* or *ex situ* with subsequent transport of the sediments into the site (see below). Ordinary fluvial deposition of the Moss Acres Racetrack sediments is contradicted by the presence of pockets of peat in unit 3. Peat is humic organic matter that accumulates in fresh water or brackish water swamps and bogs where stagnant, anaerobic conditions prevent complete oxidation and bacterial decay (Boggs, 1987; Behrensmeyer *et al*., 1992). A significant current flow into the site would have stirred up the water column and introduced oxygen to the bottom sediments unless they were considerably deeper than the current level, allowing the plant material to completely decompose. Further evidence for the absence of a current at the site is provided by the bones recovered from Moss Acres Racetrack, which show both a strong tendency towards association and a lack of any clear orientation pattern (see chapter 8).

The as noted above, the origins of the fossiliferous clay found at the Moss Acres Racetrack are unclear. On the one hand, the absence of evidence for significant fluvial deposition, the lack of sedimentary contaminants (e.g., sand), and the presence of small, pure silica grains suggest that the clay formed *in situ* from the subaerial weathering of silicate-rich (e.g., granitic) rocks. However, as pointed out by Jones (pers. comm.), the oxidizing conditions necessary for the aforementioned weathering process to occur would surely have destroyed the plant material (i.e., the peat). Thus, despite the evidence against significant fluvial deposition into the site, the clays must have somehow been transported. Jones (pers. comm.) has proposed that the clays were not transported in an ordinary fluvial fashion by surficial water, but rather were carried and deposited by flowing water moving through the aquifer, a phenomenon that is not particularly uncommon. However, this and any other hypothesis for explaining the origins of the clays in the Moss Acres Racetrack must explain the source of the silicic acid that quite likely percolated and precipitated within the clays to form silica. One possible explanation for this anomaly consistent with the aforementioned hypothesis is that the subterranean water carrying the sediment load itself contained dissolved silicic acid.

In summary, the origin of the Moss Acres Racetrack sediments can be plausibly explained by the following scenario. Earlier in the Miocene a sinkhole formed at the location of the Moss Acres Racetrack site (possibly as a response to a drop in sea level), and this sinkhole was filled by water and sediments. The ultimate source of these sediments is unclear. Scott (1988) proposed that the Alachua Formation sediments are the residue of weathered Hawthorn limestone. However, the near or complete absence here of phosphorite and heavy minerals abundant in the Hawthorn, as well as the absence of potassium-rich feldspars from the Hawthorn required to form the kaolinite found in Moss Acres Racetrack (Pirkle et al., 1965), renders this hypothesis implausible. One possible source of sediments out of which illite and kaolite could have formed is the granite-rich Appalachians to the north, though presumably the transformation of these parent minerals into clay occurred prior to their deposition in Moss Acres Racetrack. During or after this clay deposition a shallow bog or swamp came to exist in the site, a state that is reached just before the lake is completely filled during the normal pattern of fresh water lake succession. This infilling continued until the sinkhole had completely disappeared, in the final stage of lake succession merging with the adjacent topsoil. The role of unit 1 sediments in this scenario is not clear. However, its sandy character as well as the different color of its clay suggests that its origins were different from those that first filled the sinkhole.

Age

Gulf Coastal Plain fossil localities other than those of very late Pleistocene age tend to be very difficult to date directly due to the absence or near absence of useful radioisotopes in useful states (e.g., ^{40}K sealed in volcanic crystal) in sediments of the region. Strontium, specifically the $^{87}Sr/^{86}Sr$ ratio, has been used to help date some Florida localities such as the Leisey site (Webb et al., 1989); however, strontium isotope dating requires a site to have an *in situ* invertebrate fauna with diagenetically unaltered tests and represent either a marine or else at a marine/terrestrial interface facies (Elderfield, 1986), a prerequisite that Moss Acres Racetrack clearly fails. Thus, the only viable method for dating the Moss Acres Racetrack site is faunal biostratigraphic correlation, in which the fauna is dated relative to radioisotopically dated faunas in other regions, primarily the Great Plains. To facilitate this faunal analysis, a list of all mammalian taxa in the Moss Acres Racetrack fauna identified to genus or below and their chronological ranges are presented in Table 2-1.

A survey of Table 2-1 shows that almost all of the taxa present are restricted to the Clarendonian and Hemphillian land mammal ages, a chronological range of approximately 12 to about 4.5 million years (Ma) ago, or from the late Miocene to the earliest Pliocene (timescale from Hulbert, 1992, based

Table 2-1. A list of mammal taxa in the Moss Acres Racetrack fauna identified to genus or below and their chronological ranges in terms of land mammal ages.

Taxon	Chronological Range
Pliometanastes protistus	early Hemphillian[1]
Osteoborus orc	early Hemphillian[2]
Enhydritherium terraenovae	early Hemphillian-early Blancan[3]
Amebelodon britti	early-late Hemphillian[4]
Aphelops mutilis	early-late Hemphillian[5]
Dinohippus sp.	late Clarendonian-latest Hemphillian[6]
Calippus mccartyi	early Hemphillian[7]
Hipparion cf. *tehonense*	early Clarendonian-late Hemphillian[8]
Nannippus aztecus	late Clarendonian-late Hemphillian[9]
Nannippus morgani	early Hemphillian[10]
Cormohipparion emslei	early Hemphillian-late Blancan[11]
Cormohipparion plicatile	late Clarendonian-early Hemphillian[11]
Neohipparion trampasense	late Clarendonian-early Hemphillian[9]
Hemiauchenia sp.	late Clarendonian-late Rancholabrean[12]
new genus and species near *Pseudoceras*	early Hemphillian[10]
Pediomeryx hemphillensis	early-latest Hemphillian[13]

Reference abbreviations- 1: Webb and Hirschfeld, 1968; 2: Webb, 1969; 3: Berta and Morgan, 1985; 4: see chapter 3; 5: Bennett, 1977; 6: MacFadden, 1992, Hulbert, 1992; 7: Hulbert, 1988a; 8: Hulbert, 1988b; 9: MacFadden, 1984; 10: see chapter 8; 11: Hulbert, 1988c; 12: Webb et al., 1981, Kurten and Anderson, 1980; 13: Webb, 1983a.

on the radioisotopic dating and stratigraphic correlation of Great Plains faunas). *Pliometanastes* is considered diagnostic for the beginning of the Hemphillian (Tedford et al., 1987), while *Amebelodon*, *Aphelops mutilis*, *Neohipparion trampasense*, and *Pediomeryx hemphillensis* are all wide ranging taxa that are restricted to the Hemphillian (*Cormohipparion plicatile* is also restricted to the Hemphillian, but is geographically restricted to Florida [Hulbert, 1988b]). Thus the Moss Acres Racetrack can be clearly assigned a Hemphillian age, with a range from 9-4.5 Ma. No diagnostic latest Hemphillian taxa are present in the Moss Acres Racetrack fauna (e.g., *Plesiogulo*, *Felis*, *Megantereon*, *Agriotherium*), while neither *Cormohipparion plicatile* nor *Neohipparion trampasense* are known to extend into the late and/or latest Hemphillian (Schultz, 1977; Tedford et al., 1987). Thus the Moss Acres Racetrack fauna must be considered to be early Hemphillian in age, roughly 9-6 1/2 Ma. Hulbert (1988a) concluded that the Moss Acres Racetrack fauna is older than the very early Hemphillian on the basis of the following: 1) the morphologically advanced state of members of two equid species, *Nannippus aztecus* and *Cormohipparion plicatile*; and 2) the presence of *Aphelops mutilis*, a species more advanced than the late Clarendonian/early Hemphillian species *A. malacorhinus* (see also chapter 7). Thus the Moss Acres Racetrack fauna can be assigned a late early Hemphillian age, approximately 7 Ma old. At this age it is younger than such very early

Hemphillian Florida sites as Mixon's Bone Bed and McGeehee, circa 9-8 Ma, but older than such classic Great Plains late Hemphillian faunas as Rhinoceros Hill (Kansas) and Coffee Ranch (Texas), circa approximately 6-5 Ma (Tedford et al., 1987; Bennett, 1977; see chapter 3).

The Moss Acres Racetrack fauna strongly resembles another Marion County late Miocene fauna, the Withlacoochee River 4A , sharing the following taxa: *Pliometanastes protistus* (see chapter 5), *Osteoborus orc* (see chapter 8), *Enhydritherium terraenovae* (see chapter 4), *Aphelops mutilis* (Becker, 1985), *Calippus mccartyi* (see chapter 8), *Hipparion* cf. *tehonense* (Hulbert, 1988b), *Nannippus aztecus* (Becker, 1985), *Nannippus morgani*. (see chapter 8), and a new genus and species near *Pseudoceras* (see chapter 8)..Of these taxa, *Osteoborus orc*, *Calippus mccartyi*, *Nannippus morgani*, and possibly the *Pseudoceras*-like animal are endemic to these two faunas (see chapter 8). This resemblance and associated endemicism strongly suggests that these two faunas are close in age as well as location. The presence of the ursid *Indarctos* in the Withlacoochee River 4A fauna, a taxon diagnostic for the late early Hemphillian (Tedford et al., 1987), supports a late early Hemphillian age for both of these faunas. The Withlacoochee River 4A fauna will be discussed further in future chapters.

CHAPTER 3
A REDIAGNOSIS OF THE GENUS *AMEBELODON* (PROBOSCIDEA, GOMPHOTHERIIDAE) WITH A NEW SUBGENUS AND SPECIES, *AMEBELODON* (*KONOBELODON*) *BRITTI*, FROM THE MOSS ACRES RACETRACK SITE

The shovel-tusked gomphotheres represent one of the most distinctive of the proboscidean groups. As indicated by their monicker, the shovel-tuskers are characterized by broad and flat lower tusks that resemble the heads of shovels. The shovel-tuskers include such well known genera as *Amebelodon*, *Platybelodon*, and *Torynobelodon*.

The genus *Amebelodon* has been the subject of considerable systematic dispute since it was established by Barbour (1927). It has been considered both monophyletic (e.g., Gregory, 1945) and polyphyletic (e.g., Bennett, 1977) by different authors. The controversy stems from a failure to arrive at a clear diagnosis for the genus; some specimens referred to *Amebelodon* possess characters considered diagnostic for other shovel-tusker genera, *Platybelodon* and *Torynobelodon*, and have been linked to these genera by some authors. *Amebelodon* fossils described by Gaziry (1987), as well as numerous and exceptionally preserved *Amebelodon* fossils from the Moss Acres Racetrack site (Hemphillian) in North Florida, help resolve this controversy and provide a basis for a rediagnosis and taxonomic revision of the genus.

On the basis of this rediagnosis a new subgenus, *Amebelodon* (*Konobelodon*), and a new species, *A.* (*K.*) *britti*, are established.

Measurements were made with the following devices: dial calipers, tree calipers, and an anthropometer. Dental terminology follows that of Tobien (1973).

Systematics

Order Proboscidea

Family Gomphotheriidae Cabrera, 1929

Genus *Amebelodon* Barbour, 1927

Subgenus *Amebelodon* (*Amebelodon*) Barbour, 1927

Type species: *Amebelodon* (*Amebelodon*) *fricki* Barbour, 1927.

Included species: *Amebelodon* (*A.*) *floridanus* Leidy, 1886; *A.* (*A.*) *hicksi* Cook, 1922; *A.* (*A.*) *paladentatus* Cook, 1922; *A.* (*A.*) *sinclairi* Barbour, 1930.

Diagnosis: Trilophodont intermediate cheek teeth (defined in this paper as DP4, M1, and M2); lower tusks with a simple, laminated internal structure; and M3's with five or fewer lophs(ids).

Remarks: The subgenus *Amebelodon* (*Amebelodon*) encompasses all of the species traditionally referred to the genus *Amebelodon*. Its diagnostic characters are plesiomorphies shared with typical gomphotheres such as *Gomphotherium*.

Subgenus *Amebelodon* (*Konobelodon*) New Subgenus

Type species: *Amebelodon* (*Konobelodon*) *britti* New Species

Included species: *Amebelodon* (*K*.) *cyrenaicus* Gaziry, 1987.

Etymology: *Konos*, Greek for cone, refers to the dentinal rods, tapered to form cones, found in the lower tusks of this subgenus.

Diagnosis: Tetralophodont second molar; permanent lower tusks with internal dentinal rods; M3's with six well developed lophs(ids); lower tusk dentinal rods with a distinctive morphology, relatively narrow and structurally distinct near the proximal end of the tusk, expanding and tending to merge towards the distal tip; mandibular morphology and size resembles *Amebelodon* (*A*.) *fricki*, though generally somewhat larger.

Remarks: The subgenus *Amebelodon* (*Konobelodon*) includes those *Amebelodon* specimens convergent with the shovel-tusker genera *Platybelodon* and *Torynobelodon* in having tetralophodont M2's (absent from the holotype of the subgenus type species, but present on referred material T.M.M. 31075-1 and K.U.M. 3852 [Barbour and Hibbard, 1941; Gregory, 1945]) and having dentinal rods in the permanent lower tusks (the condition of the deciduous lower tusks is unknown). *Amebelodon* (*K*.) *cyrenaicus* is included in the subgenus despite having two plesiomorphic features: tusks with internal lamination and a trilophodont M1 (DP4 is unknown for this species) (Gaziry, 1987). Though resembling the subgenus *A*. (*Amebelodon*) in these plesiomorphic features, the presence of dentinal rods in the medulla of these tusks as well as the tetralophodont second molar clearly place *A. cyrenaicus* in the subgenus *A.* (*Konobelodon*).

Amebelodon (*Konobelodon*) *britti* New Species.

Synonyms: *Amebelodon* (*Amebelodon*) *fricki* Osborn and Granger, 1931; Barbour and Hibbard, 1941; Gregory, 1945.

Etymology: Named for R. Jerry Britt, Jr., a deceased graduate student at the University of Florida, in honor of his contributions to Florida paleontology.

Diagnosis: Internal lamination absent from the lower tusks, with both the cortex and medulla solidly filled with dentinal rods; M1 tetralophodont.

Holotype: UF 70000, a partial mandible lacking most of the symphysis and the lower tusks and possessing only the M3, and associated fragments of the hyoid apparatus, the atlas and axis vertebrae, and the centrum of an indeterminate cervical vertebra, in the collection of the Florida Museum of Natural History.

Paratypes: UF 69994, an intact upper tusk, and UF 97269, a completely intact lower tusk with the root preserved, in the collection of the Florida Museum of Natural History.

Referred material: *Amebelodon* from the Rhino Hill site, Kansas (K.U.M. 3852, reconstructed palate with the M2's and M3's; K.U.M. 3477, juvenile palate with DP4 and M1; K.U.M. 2865 and K.U.M. 3858, free molars; K.U.M. 3853 and K.U.M 3854, lower tusks; and K.U.M. 3855, K.U.M. 33597, K.U.M. 33598, and K.U.M. 33599, upper tusks, Museum of Natural

History, University of Kansas); mandible from the Parcell Ranch in Texas (T.M.M. 31075-1, Texas Memorial Museum at Austin); an isolated lower tusk fragment from Texas (D.M.N.H. 1319, Denver Museum of Natural History); material from the Moss Acres Racetrack site (UF 135286, mandible with one partial lower tusk; UF 69995, UF 97268, UF 124373, UF 135802, lower tusks; UF 69998, the distal half of an upper tusk; UF 97261, partial upper tusk; UF 69993, an isolated mandibular symphysis; three unprepared and uncatalogued skulls; and assorted post-cranial elements including limb bones, Florida Museum of Natural History in Gainesville, Florida- see Appendix 1); and a lower M3 from the Bone Valley region of Central Florida (UF 95778, Florida Museum of Natural History in Gainesville, Florida).

Description

Holotype, UF 70000

The most diagnostic of the holotype specimens is the partial mandible (Figure 3-1). Two M3's are present, without even an alveolus to indicate the nature of the M2's. When originally recovered, this specimen was badly crushed mediolaterally; its present three dimensional econstruction is the result of extensive restoration work at the Florida Museum of Natural History. Measurements of the specimen are presented in Table 3-1. The symphysis is poorly preserved. Most of the symphysis ends approximately at the anterior end of the symphyseal ridge; where the symphysis is broken, the

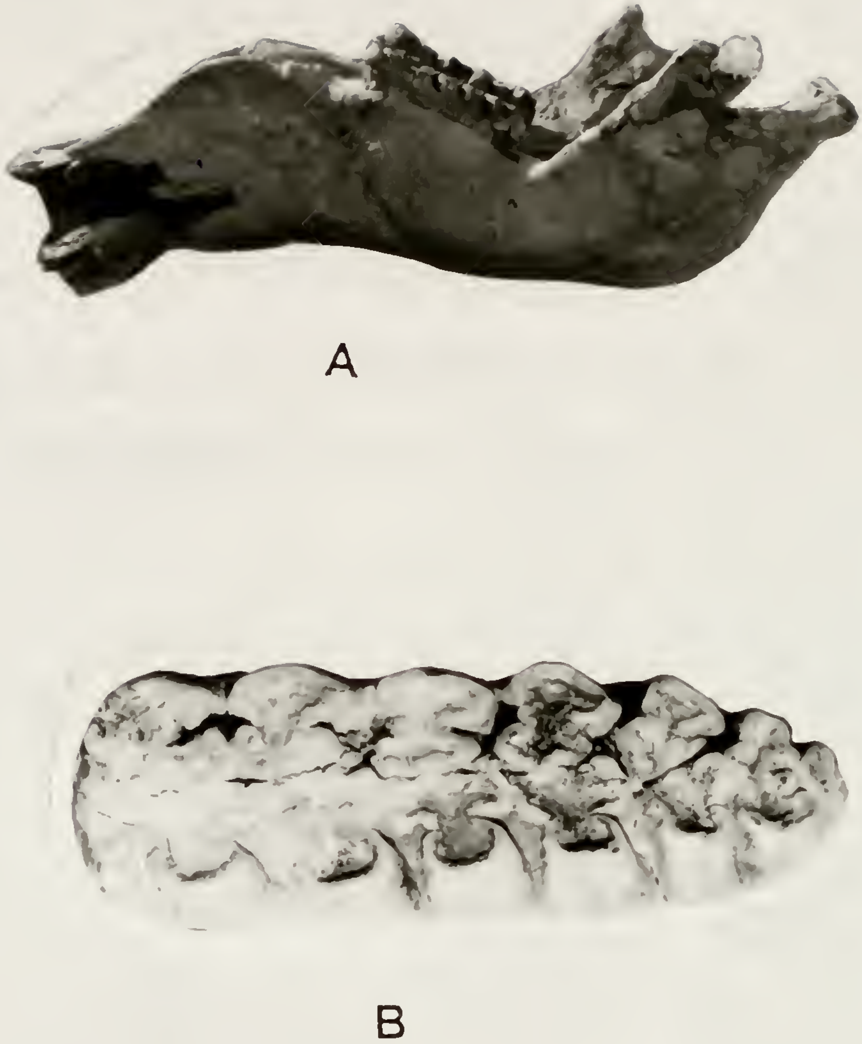


Figure 3-1. Mandible UF 70000, holotype specimen of *Amebelodon* (*Konobelodon*) *britti*. A) dorso lateral view; B) close-up of the left M3, occlusal view.

Table 3-1. Measurements (millimeters) of the partial mandible UF 70000, Amebelodon (Konobelodon) britti, with comparative measurements of the type specimen of Amebelodon (Amebelodon) fricki, UNSM 1226.

	UF 700000	UNSM 1226
total length:	1384*	2133
length from condyle to the edge of the symphyseal ridge:	985	
length from coronoid to condyle:	272	
intercondylar width:	555	508
condylar width:	157	
height of symphyseal ridge at proximal edge:	301	
maximal width of symphyseal ridges:	139	
maximal height of symphyseal ridges (from symphyseal floor):	70	
depth from coronoid to angular process:	375	356
length of third molar:	286	229
width of third molar	90	89

* specimen broken and value not indicative

posterior sections of the lower tusk alveoli are exposed. The medial alveolar wall is missing except deep in the symphysis near the posterior walls of the alveoli. The tusks are largely missing; however, some tusk material remains within the alveoli

distinctly showing the dentinal rods in the internal structure. The suprasymphyseal ridges differ from those of the type mandible of _A_. (_A_.) _fricki_ (UNSM 1226) and also from the referred _A_. (_K_.) _britti_ mandible (T.M.M. 31075-1) by rising high above the symphyseal margin and having a distinct lateral flare.

The right lower M3 is badly damaged. Discussion of the molars will be based largely on the left M3, which is almost perfectly preserved. One of the most striking aspects of these molars is their extreme length. The left molar is 286 mm long, considerably longer than the lower M3 of the type specimen of _A_. _fricki_ (229 mm, from Barbour, 1929), and the upper M3 numbered K.U.M. 3852 (236 mm, value from Barbour and Hibbard, 1941). The M3's have six lophids, small cingula, and small talonids. The lophids are highly worn, so that most of the detail of the morphology of the conids and conulids has been lost; however, the remaining enamel folds comprising the lophids remain intact. The ectolophids have highly developed trefoils. The conid-derived fold of the trefoil is broad, with a distinct constriction where the fold meets the rest of the trefoil; the conulid-derived folds are medio-laterally compressed and antero-posteriorly elongated. The entolophids are incipiently trefoiled. The conid-derived fold is broad, medio-laterally compressed, and elongated antero-posteriorly. The conulid-derived folds are small, resulting in a poorly developed trefoil pattern.

The rest of this partial mandible resembles the type mandible of *A. fricki* in size and morphology. This specimen is distinctly larger than the type of *A. fricki*, but the differences are not great (as shown in Table 3-1). There is a strong resemblance between the two specimens in such features as the mandibular condyle, the coronoid process, the angular process, and the horizontal and vertical mandibular rami.

Paratype, UF 69994

This specimen is a right upper tusk (Figure 3-2). Its overall preservation is excellent; however, it has sustained three major breaks. Measurements of the specimen are presented in Table 3-2.

A large enamel band extends along the lateral surface of the tusk (orientation references will assume that the tusk is in its life position, oriented perpendicular to the ground). The enamel band is present throughout the length of the tusk, though the preservation is not uniform. It is largely intact over the distal one-third of the tusk, and shows varying degrees of post-mortem stripping over the proximal two-thirds of the tusk length. Where the enamel has been stripped, a distinct scar remains to show its former presence. A facet is

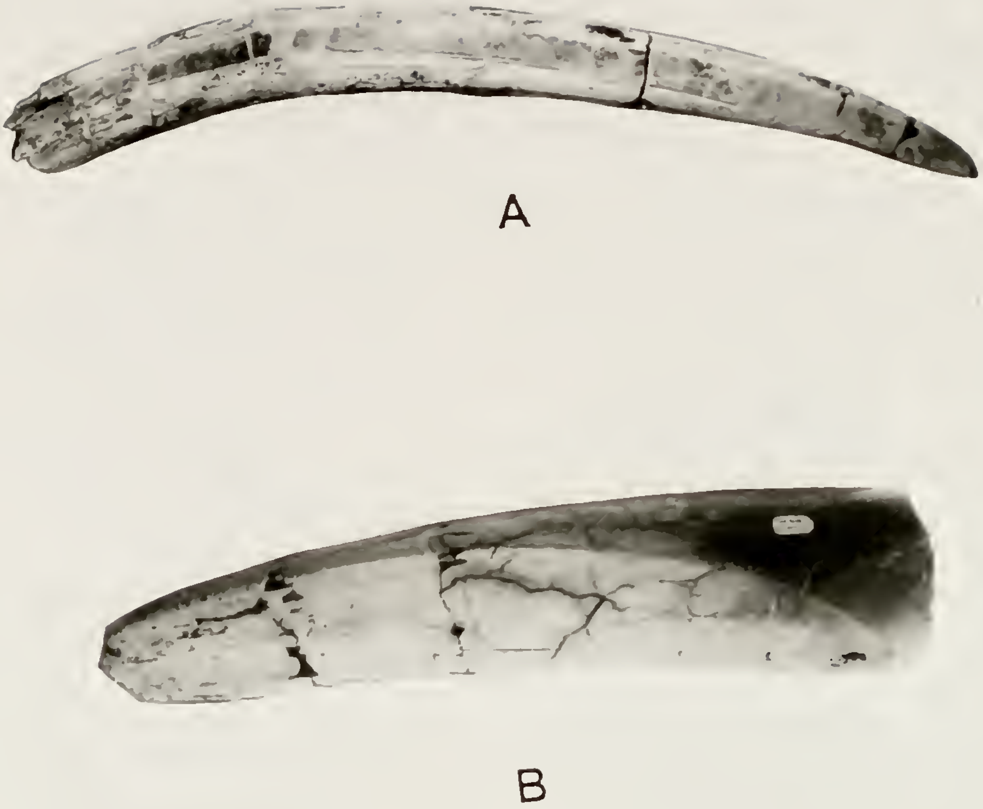


Figure 3-2. UF 69994, right upper tusk, paratype of *Amebelodon* (*Konobelodon*) *britti*. A) lateral view; B) close-up of the medioproximal wear facet.

Table 3-2. Measurements (millimeters) of UF 69994, a right upper tusk of *Amebelodon* (*Konobelodon*) *britti*.

total length:	1570
maximum anteroposterior diameter:	284
width of enamel band:	66
length of wear facet:	566

present on the medial surface of the distal end of the tusk, extending 566 mm from its tip. The facet does not lie flat on the medial surface, but rather is heavily slanted, forming a thin edge at the latero-posterior surface of the tusk. The proximal portion of the facet is directly bounded at the latero-posterior surface by the enamel band, forming an apparent cutting edge. Where it bounds the facet the enamel band is highly crenulated, possibly the result of abrasion. The facet, with its enamel bordered cutting edge, may be the result of wear caused by bark stripping and perhaps vegetation cutting behavior (functional and ecological aspects of this facet and similar facets in other gomphotheres are discussed in detail in Lambert, 1989; 1992).

Paratype, UF 97269

This specimen is a right lower tusk, excellently preserved (Figure 3-3). However, it has sustained a break, repaired with plaster, 830 mm from its proximal tip. Measurements of the specimen are presented in Table 3-3.

The tusk is extremely flattened dorso-ventrally, with a very shallow dorsal concavity. The lateral edge is far thicker than the medial edge, giving the tusk a cross-sectional profile similar to the type specimen of A. fricki. Medio-laterally the tusk is gently curved sigmoidally, the curvature becoming sharp at the proximal end of the tusk. The tusk is also gently curved sigmoidally in dorso-ventral aspect, again becoming sharp at the proximal end. The tusk

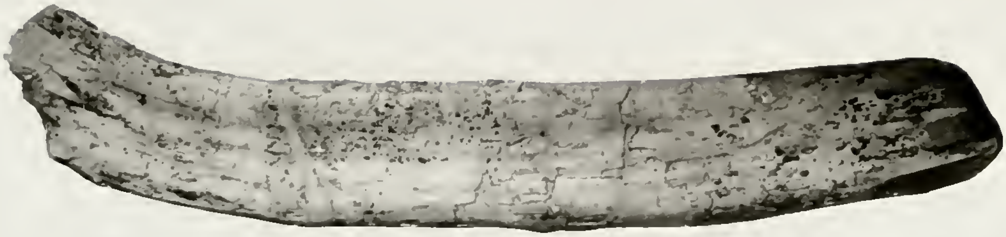


Figure 3-3. UF 97269, right lower tusk, paratype of *Amebelodon* (*Konobelodon*) *britti*.

Table 3-3. Measurements (millimeters) of UF 97269, a right lower tusk of *Amebelodon* (*Konobelodon*) *britti*.

total length:	1236
maximum width:	175
thickness at inner border:	30
thickness at outer border:	55

has a well preserved root, which is extremely flattened relative to the rest of the tusk. No dentinal rods are directly exposed in this specimen. However corrugations, which are more obvious on the proximal than the distal regions, reveal their presence.

Skull

Three *Amebelodon britti* skulls were recovered from the Moss Acres Racetrack during the 1991 field season, the first reasonably well preserved skulls ever found for the genus *Amebelodon*. Preparation of these specimens is in progress, so that a detailed description is currently impossible. However, preliminary preparation of one skull reveals heavily retracted nasal bones, considerably more retracted than those of modern elephants. This retraction indicates that *Amebelodon britti*, and possibly *Amebelodon* as a whole, had a large, well developed proboscis, possibly larger than that of modern elephants (see Lambert, 1992 for further discussion).

Post-cranial Skeleton

The Moss Acres Racetrack *Amebelodon britti* material is exceptional in containing a variety of post-cranial elements, especially limb bones, from a single population. The manus and pes are especially well represented, with nearly or fully complete associated specimens known. Table 3-4 provides measurements of some of the major limb bones, and Appendix 1 contains a complete list of post-cranial material so far recovered from Moss Acres Racetrack.

Table 3-4. Measurements (millimeters) of *Amebelodon* (*Konobelodon*) *britti* post-cranial elements.

UF 69997			
	left radius		
		total length:	800
	left ulna		
		total length (including olceranon):	890
	right scapula		
		total length along spine:	836
	right tibia		
		total length:	744
		minimum shaft width:	94
		width across distal articulating surface:	265
		width across proximal articulating surface:	196
	right fibula		
		total length:	679
	right femur		
		total length:	1297
		length from ball to greater trochanter:	433
		width across condyles:	244
		minimum mediolateral shaft width:	150
		minimum anteroposterior shaft width:	109
UF 69944			
	right pelvis		
		maximum length from ischium to ileum ramus edge:	542

Limb bone measurements allow me to estimate the original height and weight of this animal. The forelimb is incomplete for the partial skeleton UF 69997, lacking a humerus; thus, a shoulder height cannot be directly determined for this individual. However, the hindlimb is complete, allowing me to estimate its pelvic height as approximately 2.3-2.7 meters. The height at the shoulder was probably not greatly different. This figure suggests that this animal was roughly similar in height to a modern Asian elephant (Elephas maximus) (Nowak and Paradiso, 1983). However its mass, based on a femoral regression (see chapter 10), has been estimated at approximately 10,000 kilograms, a figure in the size range of a Columbian Mammoth (Mammuthus columbi) (Shipman, 1992). Thus, Amebelodon britti may have been one of the largest mammals to ever walk in North America.

The Rediagnosis of Amebelodon

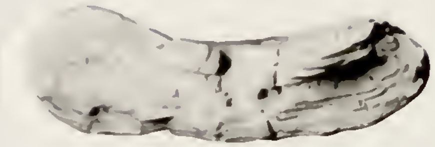
The confusion over the correct diagnosis of Amebelodon has its basis in a failure by many authors to properly evaluate the phylogenetic nature of two features considered diagnostic for the genus by many authors: internal structure of the lower tusks, and number of lophs(ids) on the intermediate cheek teeth. The genus Amebelodon is traditionally diagnosed by the following characters: (1) a narrow, extremely elongated mandibular symphysis; (2) elongated, narrow, flattened lower tusks with a shallow dorsal concavity; (3) lower tusks with an internal structure composed of simple concentric lamina (see Figure 3-4A); and (4) intermediate cheek teeth with three lophs(ids), a condition known as trilophodonty (Barbour, 1929; Gregory, 1945; Osborn, 1936; Tobien, 1972). However, shovel-tusker lower material has been referred to the *Amebelodon* genotypic species, *A. fricki*, on the basis of overall similarity despite the presence of the following characters: (1) lower tusks with an internal structure composed of tightly packed dentinal rods such as found in *Platybelodon* (see Figure 2-4C), and (2) tetralophodont intermediate cheek teeth (Osborn and Granger, 1931; Barbour and Hibbard, 1941; and Gregory, 1945). This character combination is considered diagnostic for *Platybelodon* and *Torynobelodon* rather than *Amebelodon* (Gregory, 1945).

Thus, there is a clear conflict as to the proper diagnosis of *Amebelodon*. This conflict leads to two possible conclusions.

(1) The traditional diagnosis of *Amebelodon* involving lower tusk internal structure and loph number of the intermediate cheek teeth is erroneous. Only mandibular symphyseal morphology and superficial lower tusk morphology can be used to diagnose the genus, while lower tusk internal structure and M2 loph number divide the genus into two distinct morphotypes, one of which is convergent with *Torynobelodon* and *Platybelodon* (here placed in the subgenus *Amebelodon* [*Konobelodon*]).

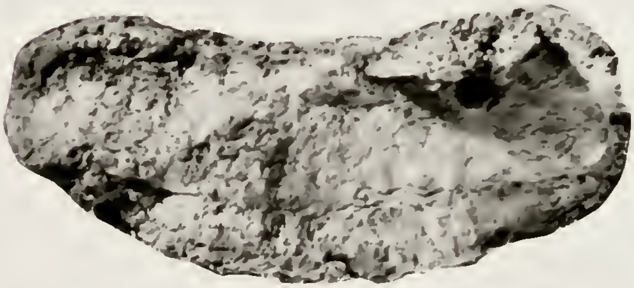
Figure 3-4. Cross-sectional views of lower tusks from different *Amebelodon* species demonstrating differences in internal structure. A) *Amebelodon* (*Amebelodon*) sp., showing a simple lamination plesiomorphic for gomphotheres; B) *Amebelodon* (*Konobelodon*) *cyrenaicus*, showing both internal lamination (cortex) and densely packed dentinal rods (medulla); and C) *Amebelodon* (*Konobelodon*) *britti*, showing uniform, densely-packed dentinal rods.

A



B

C



(2) The traditional diagnosis of *Amebelodon* is correct. The anomalous specimens that conflict with the traditional diagnosis of *Amebelodon* do not actually belong to the genus but rather are more closely related to *Torynobelodon* and *Platybelodon*, and are only convergent with *Amebelodon* in certain features.

Both conclusions have been drawn by different authors, the former by Gregory (1945) and the latter by Bennett (1977). Evidence favoring the first conclusion exists in the intermediate molar loph numbers of the taxa in question. *Platybelodon* (and presumably *Torynobelodon*) are tetralophodont in all of their intermediate molars, though the M1's of some individuals may have only three lophs(ids)(Osborn, 1936). However, the least derived of the anomalous *Amebelodon* species, *A. cyrenaicus*, is only tetralophodont in its M2; its M1 is definitely known to be trilophodont (Gaziry, 1987). The more derived anomalous *Amebelodon* species, *A. britti*, has both a tetralophodont M2 and M1. Moreover, its DP4 is trilophodont in contrast to the tetralophodont DP4's of *Platybelodon*/*Torynobelodon* (Mebrate, 1987; Osborn, 1936). This situation is consistent with a scenario of convergence between the two groups.

Additional evidence for convergence between these groups is found in the internal structure of the lower tusks of *A. cyrenaicus*. Figure 3-4A shows an *Amebelodon* lower tusk with the internal lamination plesiomorphic for *Amebelodon* and gomphotheres as a whole. Figure 3-4C shows an anomalous

Amebelodon lower tusk that is solidly filled with dentinal rods, a derived condition shared with *Platybelodon*/*Torynobelodon* (see Figure 3-5). However, *A. cyrenaicus*, shown in Figure 3-4B, reveals a lower tusk condition clearly intermediate between those shown in Figures 3-4A and 3-4C. Its cortex has the simple lamination plesiomorphic for *Amebelodon* and gomphotheres as a whole, while its medulla is solidly filled with dentinal rods identical to those found in the derived lower tusks of the anomalous *Amebelodon* specimens. Thus, *A. cyrenaicus* plausibly represents an intermediate stage between the two *Amebelodon* morphotypes. This indicates that the derived character state shared between the anomalous *Amebelodon* morphotype and that of *Torynobelodon*/*Platybelodon* is analogous, and therefore that the traditional diagnosis of *Amebelodon* based on this character state is erroneous. Additional evidence for the analogy of this character state exists in the detailed morphology of the dentinal rods found in the two groups (see below).

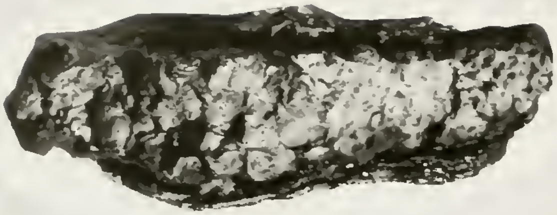
Since I have shown the traditional diagnosis of *Amebelodon* to be untenable, a new diagnosis must be formulated, requiring not a drastic revision of the original diagnosis but rather a simplification. The genus *Amebelodon* can be diagnosed by: (1) a narrow, extremely elongated symphysis (more so than in *Gomphotherium*); and (2) elongated, narrow, dorso-ventrally flattened tusks with shallow dorsal concavities.

Dentinal Rods

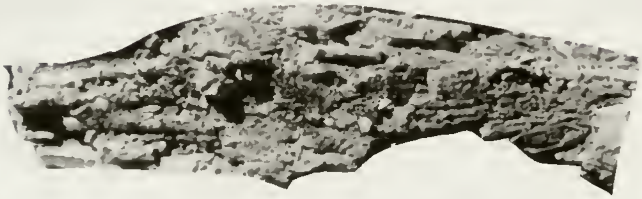
In the preceding section it was shown through the evidence of the gross morphology of the intermediate molars and lower tusk internal structure that the genus *Amebelodon* contains two morphotypes, one convergent with *Platybelodon* and *Torynobelodon*. This conclusion is further supported by differences between these groups in the morphology of the individual dentinal rods within their lower tusks.

In the study, four *Amebelodon* (*Konobelodon*) *britti* lower tusk specimens from Moss Acres Racetrack site and eleven *Torynobelodon* sp. lower tusk fragments from the Withlacoochee 4A site (North Florida, early late Hemphillian) were examined (all specimens are from the collection of the Florida Museum of Natural History). This examination revealed the following aspects of *Torynobelodon* dentinal rod morphology. The rods are all densely packed within the external shell of the tusk. The individual rods are structurally indistinct, and tend to merge into themselves in cross-section (Figure 3-5A). From a side view, the dentinal rods are extremely difficult to resolve, resembling solid dentine. The dentinal rods had this same appearance in all of the examined specimens, indicating that the dentinal rod morphology is essentially uniform throughout the lower tusks of *Torynobelodon*. A similar morphology can be seen in the lower tusk of *Platybelodon* sp. described by Maglio (1969, figure 2).

Figure 3-5. Views of dentinal rods in *Torynobelodon* and *Amebelodon britti* lower tusks. A) *Torynobelodon*, unknown tusk region, cross-sectional view; B) *Amebelodon britti*, lateral view near the tusk root; and C) *Amebelodon britti*, cross-sectional view near the distal though not distalmost end.



A



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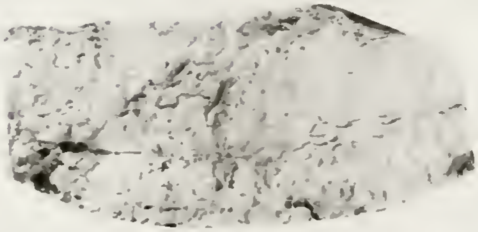


C

The dentinal rods of *Amebelodon* (*Konobelodon*) *britti* differ from those of *Platybelodon*/*Torynobelodon* in being morphologically heterogeneous throughout the tusks. At the proximal region of the tusks, the dentinal rods are extremely thin and have clear boundaries, being distinct in cross-sectional view. Similarly, the proximal dentinal rods are visible in lateral view, appearing as distinctly layered strands (Figure 3-5B). A distal progression along the tusk reveals an orderly change in the nature of the dentinal rods; the rods become wider and begin to merge, approaching the condition found in *Platybelodon* and *Torynobelodon* (Figure 3-5C). At the very distal end of the tusk, the dentinal rods completely disappear and are replaced by undifferentiated solid dentine. The pattern just described for the *A*. (*K*.) *britti* lower tusk material from Moss Acres Racetrack site has also been documented for other *A*. (*Konobelodon*) lower tusk specimens, notably those studied by Gregory (1945) and Gaziry (1987). Thus, the morphological differences between the individual dentinal rods of *A*. (*Konobelodon*) and *Platybelodon*/*Torynobelodon* offer strong evidence for their analogous nature in addition to that supplied by lower tusk gross morphology.

However, the premise of dentinal rod analogy in these two groups raises a legitimate question. How and why the did this unusual condition evolve in parallel? These two questions are interconnected. Both *Amebelodon* and

Platybelodon/Torynobelodon are characterized by lower tusks that are broad and dorso-ventrally thin, and therefore presumably more vulnerable to breakage than the deeper, more rounded tusks typical of gomphotheres. A commonly proposed functional explanation for the evolution of these dentinal rods involves internal bracing to resist breakage (e.g., Osborn and Granger, 1931). If this plausible but so far untested proposal is correct, then it is not terribly surprising that shovel-tusked gomphotheres evolved parallel adaptations in the face of this common selective pressure.

However, the question arises as to why these two gomphothere groups independently evolved a bracing mechanism as unusual as dentinal rods, an adaptation so far unknown in any other gomphothere groups. A purely speculative answer to this question may lie in the nature of mammalian tooth development. The tusks (canines) of walruses (Odobenidae) contain an internal cavity that is packed with distinct though irregularly arranged pieces of dentine, known as globular osteodentine, that is superficially similar in appearance to the dentinal rods of Torynobelodon and Platybelodon lower tusks (Ray, 1960). Walrus tusks are used as grasping devices during locomotion on ice, and must endure enormous stress (Nowak and Paradiso, 1983). Presumably the globular osteodentine is an adaptation to help these tusks resist breaking. The presence of apparently similar dentinal structures in such phylogenetically distant animals as the gomphothere proboscideans and the carnivore walrus suggests that the potential to form distinct internal dentinal structures above the dentinal tubule level is common to mammalian teeth in general. Thus, the evolution of dentinal rods in *A*. (*Konobelodon*), *Platybelodon*/*Torynobelodon*, and similar dentinal structures in walruses may represent separate responses by common developmental systems to a common selective pressure, the need to prevent elongated tooth breakage by shearing forces.

The evolution of dentinal rods in the *Platybelodon*/*Torynobelodon* lineage can be explained as a simple structural adaptation linked to the evolution of extremely flattened lower tusks (their tusks are relatively much thinner than those of *Amebelodon*). However their evolution within the genus *Amebelodon* is more difficult to explain, since species within the subgenus *Amebelodon* (*Amebelodon*) apparently managed well without dentinal rods. *A priori* the most plausible explanation for the evolution of dentinal rods in A. (*Konobelodon*) is that a change in feeding habits involving the lower tusks of individuals in this clade resulted in greater lower tusk stress. However, a study by Lambert (1989) of *Amebelodon* lower tusk wear patterns and their feeding habit implications found no significantly different trends between *A*. (*Amebelodon*) and *A*. *Konobelodon* individuals. Within both subspecies some individuals (the behavioral variation was as great within as between species) used their lower tusks in behaviors that must have been highly stressful, for example mandibular shoveling, and shaving bark from trees with the tip of the tusk. Thus, the evidence casts strong doubt on this hypothesis.

Another possible explanation could involve simple structural engineering such was proposed for *Platybelodon* and *Torynobelodon* above. A change in lower tusk size and/or shape in members of the *A*. (*Konobelodon*) clade could have resulted in a need for increased internal bracing. However, the lower tusks of some *A*. (*Konobelodon*) individuals are similar to or even smaller in size than those of *A*. (*A*.) *fricki*, which lacks dentinal rods (Gregory, 1945). Moreover, in cross-sectional profile the lower tusks of *A*. (*Konobelodon*) individuals strongly resemble those of *A*. (A.) *fricki*. Thus the evidence fails to support this hypothesis as well. I have no other plausible explanation to offer, and for now the evolution of dentinal rods in the *A*. (*Konobelodon*) lineage remains an enigma.

Biogeography and Chronology

Known records of the subgenus *Amebelodon* (*Konobelodon*) are quite circumscribed both biogeographically and chronologically. The earliest record of the subgenus *A*. (*Konobelodon*) is the species *A*. (*K*.) *britti* from Moss Acres Racetrack, which is late early Hemphillian age, about seven million years old (see chapter 2). *Amebelodon*. (*K*.) *britti* is also known from the Rhino Hill site in Kansas, which Bennett (1977) correlated with the Coffee Ranch fauna of

Texas. Tedford et al. (1987) gave the latter fauna an early late Hemphillian age, about six million years old. *A.* (*K.*) *britti* is also known from the Bone Valley region of central Florida. In Texas specimens occur both from an unknown site (Osborn and Granger, 1931), and the Panhandle (Gregory, 1945). None of these latter specimens has a sufficient biostratigraphic record to provide an accurate faunal correlation, though in each instance a Hemphillian age is most likely.

In North America, *Amebelodon* became extinct in the late Hemphillian (latest Miocene), along with much of the Clarendonian ungulate chronofauna (terminology of Webb, 1983). *Amebelodon* is unknown from faunas younger than that of the Coffee Ranch in North America. In the Old World, *A.* (*Konobelodon*) is known only by the species *A.* (*K.*) *cyrenaicus* from the Sahabi fauna of North Africa, believed to be earliest Pliocene (Ruscinian) (Gaziry, 1987; Tobien, 1986). This record of *A.* (*K.*) *cyrenaicus* represents the youngest record of *Amebelodon* known. Overall, the genus *Amebelodon* is rare in the Old World, known by only two other isolated lower tusk specimens, one from Turkey and the other from China. Both specimens belong to the subgenus *A.* (*Amebelodon*), with one referred to *A.* (*A.*) *fricki* (Tobien, 1986).

CHAPTER 4
THE OSTEOLOGY, PALEOECOLOGY, AND PHYLOGENY OF THE GIANT OTTER *ENHYDRITHERIUM TERRAENOVAE*

The otters, both living and extinct, can be placed into two distinct groups based on the relative robustness of their carnassial cusps. One of these groups includes most of the living *Lutra*-like genera as well as the extinct genus *Satherium*, and is characterized by carnassials with relatively slender cusps that tend to form blades, especially the paracone and metacone on the upper fourth premolar. These otters were loosely named the "fish-eating" otters by Repenning (1976). The other group is characterized by carnassials with relatively thick enamel and bulbous cusps that show no tendency to merge into blades. This group, including the living genus *Enhydra* as well as the extinct genera *Enhydriodon* and *Enhydritherium*, was loosely named the "crab-eating" otters by Repenning (1976), a reference to the presumed durophagous diet of its members (henceforth in this paper when referring to this group, the morphologically descriptive term bunodont will replace the term "crab-eating").

The extinct bunodont otters can be divided into distinct Old World and New World taxa. The Old World bunodont otters are all referable to the genus *Enhydriodon* (the status of

Sivaonyx and its relationship to *Enhydriodon* is unclear, and it will not be further considered here; see Colbert, 1935 and Repenning, 1976). At one time the New World bunodont otters were referred to *Enhydriodon* as well, the single species *E. lluecai*. However, Berta and Morgan (1985) removed them from *Enhydriodon* and placed them into a new monospecific genus, *Enhydritherium terraenovae*.

Enhydriodon is represented by a reasonably good assortment of cranial and postcranial materials, though no one species is particularly well known. *Enhydriodon sivalensis* is known by a well preserved skull, the holotype, though no postcranial specimens have been assigned to this species (Colbert, 1935). In contrast, the limbs are well represented for the dubious species *E. latipes* described by Pilgrim (1931), though no dental or cranial elements have been referred to this species. Most of the other species of *Enhydriodon* are known on the basis of mandibular material largely consisting of the first molar, though some postcranial elements have been assigned to *E. africanus* (Repenning, 1976; Hendey, 1978).

In contrast to *Enhydriodon*, the genus *Enhydritherium* is known in the literature on the basis of extremely limited material. Berta and Morgan (1985) based their diagnosis of *Enhydritherium terranovae* on a small number of mandibular fragments and associated lower molars, isolated upper fourth premolars, and a single tibia. Although this material is adequate to distinguish *Enhydritherium* from *Enhydriodon*, it is insufficient to clarify details of its osteology, autecology, or phylogeny.

Over the years since the publication of the paper by Berta and Morgan, the Florida Museum of Natural History has accumulated a fairly extensive collection of additional Enhydritherium material. The majority of this material (in terms of individual animals represented) consists of mandibular elements (though a partial ulna has also been found) from the Bone Valley region of Central Florida (latest Hemphillian). Of far greater importance, however, is a partial skeleton of Enhydritherium terraenovae that was found at the Moss Acres Racetrack site. This specimen, bearing the number UF 100000, surpasses all other documented bunodont otter specimens in the literature, including (1) a reasonably intact skull, (2) an intact mandible, (3) a significant portion of the axial column, and (4) virtually complete fore- and hindlimbs.

This Enhydritherium terraenovae partial skeleton provides the impetus for this paper. The purposes of this study are to investigate the osteology, autecology, and phylogeny of this species in a level of detail previously impossible. Specifically, I will undertake the following three tasks:

(1) on the basis of this new specimen, describe the osteology of Enhydritherium terraenovae, and on the basis of that description expand the generic/specific diagnosis given originally by Berta and Morgan (1985);

(2) analyze the depositional environments of all *Enhydritherium* occurences and therefore determine their likely habitat preferences;

(3) interprete osteological features of *Enhydritherium* with respect to their adaptive significance in comparison with other otters;

and (4) reevaluate the phylogeny of this taxon.

Methods

In examining the osteology, phylogeny and autecology of *Enhydritherium terraenovae*, the following taxa and specimens were used for comparison:

Amblonyx cinerea: UF(M) 14791

Enhydra lutris: UF(M) 24196, UF(M) 22397, UF(M) 24197, UF(M) 24922

Lutra canadensis: UF(M) 22598

Pteronura brasiliensis: USNM(M) 304663

Satherium piscinaria: UM-V 61875

Enhydriodon sivalensis: based on the verbal diagnosis given for *Enhydriodon* in Pilgrim (1931) (skull only)

Enhydriodon latipes: based on verbal descriptions and drawings from Pilgrim (1931) (limb elements only)

Mustela vison: UF(M) 382

Zalophus californianus: UF(M) 24910

Specimens were measured with dial calipers.

Osteology

Skull

The skull of this partial skeleton was badly crushed when discovered from the field, and required extensive reconstruction for study. The dermal roof bones survived preparation in good condition. Unfortunately both the palate, excluding the maxillary region of the toothrow, and most of the basicranium were crushed beyond repair, limiting the detail with which the cranial anatomy can be discerned. The dorsal and lateral dermal bones of the cranium and rostrum are essentially intact (Figures 4-1 through 4-3). Cranial measurements are presented in Table 4-1.

The lateral profile of the skull generally resembles that of Lutra. The cranium is very low and flat, with a shallow sagittal crest. The facial region is nearly level with the cranium, while the rostrum has a gentle slope similar to that in Lutra. This differs from the condition observed in Enhydriodon sivalensis, which has a highly swollen cranium similar to that of Aonyx (Pilgrim, 1931), and Enhydra, which has a steeply sloped rostrum. An enlarged triangular process is present on the dorsal surface of the jugal (suborbital process). Similar processes were observed at the same location in the other examined otters, but these were little more than small, rounded bumps.

In dorsal view the cranium shows a distinctly rounded profile typical of otters. The frontal region is relatively broad rather than constricted as in the other otters examined

Table 4-1. Cranio-mandibular measurements (millimeters) of the *Enhydritherium terraenovae* specimen UF 100000.

Skull	
length from occipital condyle to premaxilla	155
width across mastoid process	115
occipital height from condyle to nuchal crest	53
Mandible	
length from condyle to symphysis	111
width across coronoid processes	65
height of coronoid process from ventral ramus border	51
Dentition	
upper P4 length, labial border	11.8
upper P4 length, lingual border	10.5
upper P4 width, anterior border	11.3
upper P4 width, posterior border	14.5
upper M1 length, labial border	9.4
upper M1 length, lingual border	12.4
upper M1 width, anterior border	14.1
upper M1 width, posterior border	13.5
lower M1 length down midline	15.9
lower M1 width, trigonid (metaconid-protoconid)	9.3
lower M1 width, talonid	10.4

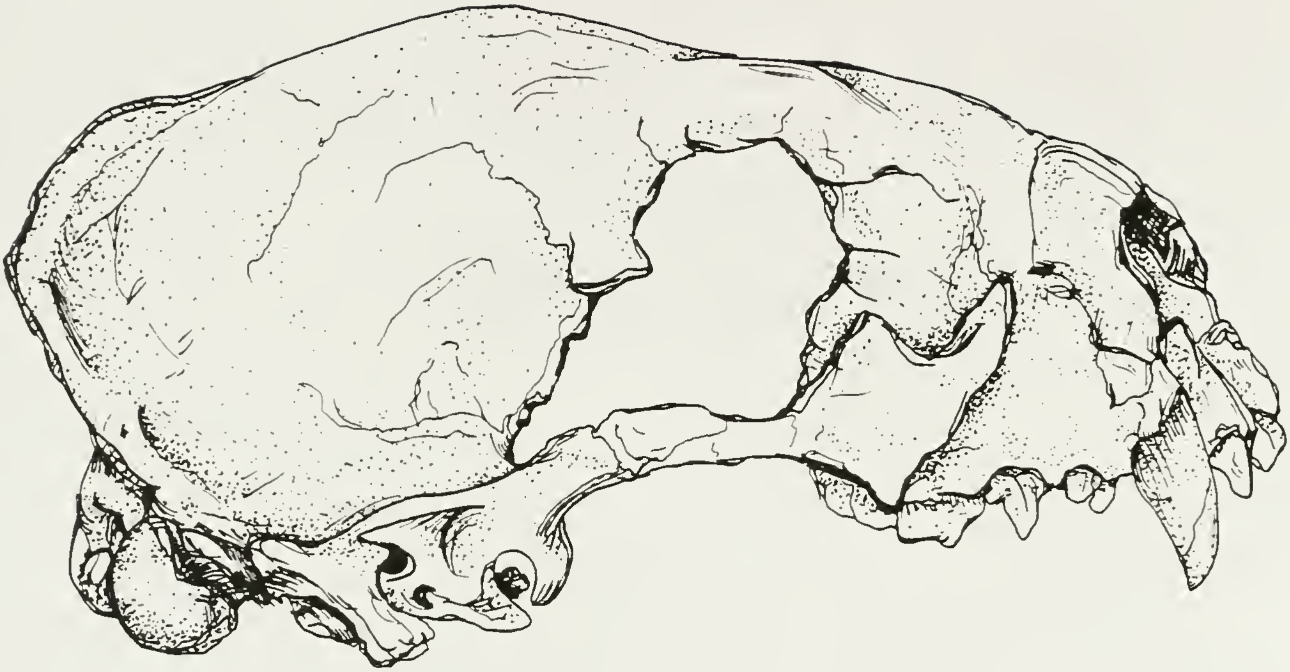


Figure 4-1. Enhydritherium skull, lateral view.

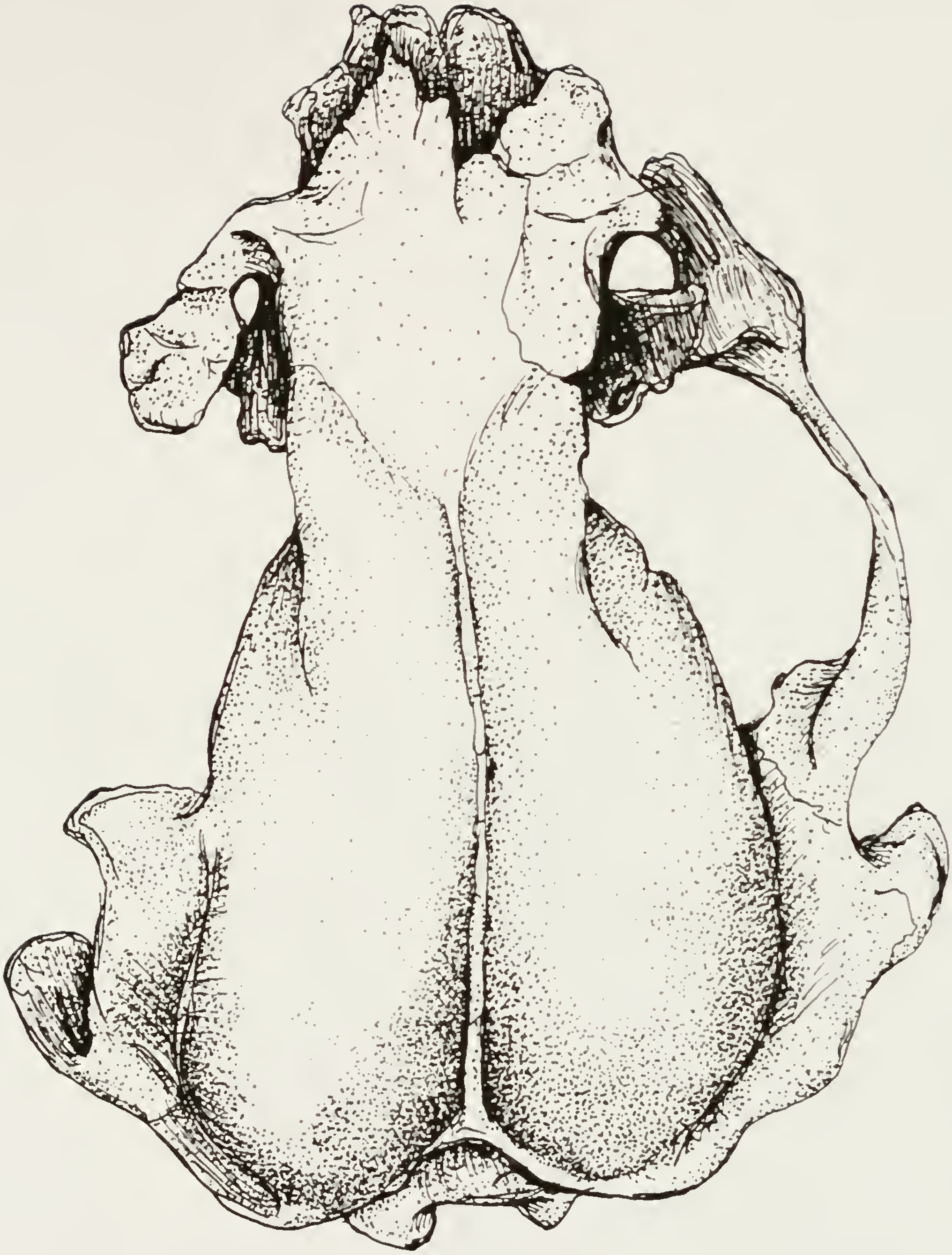


Figure 4-2. Enhydritherium skull, dorsal view.

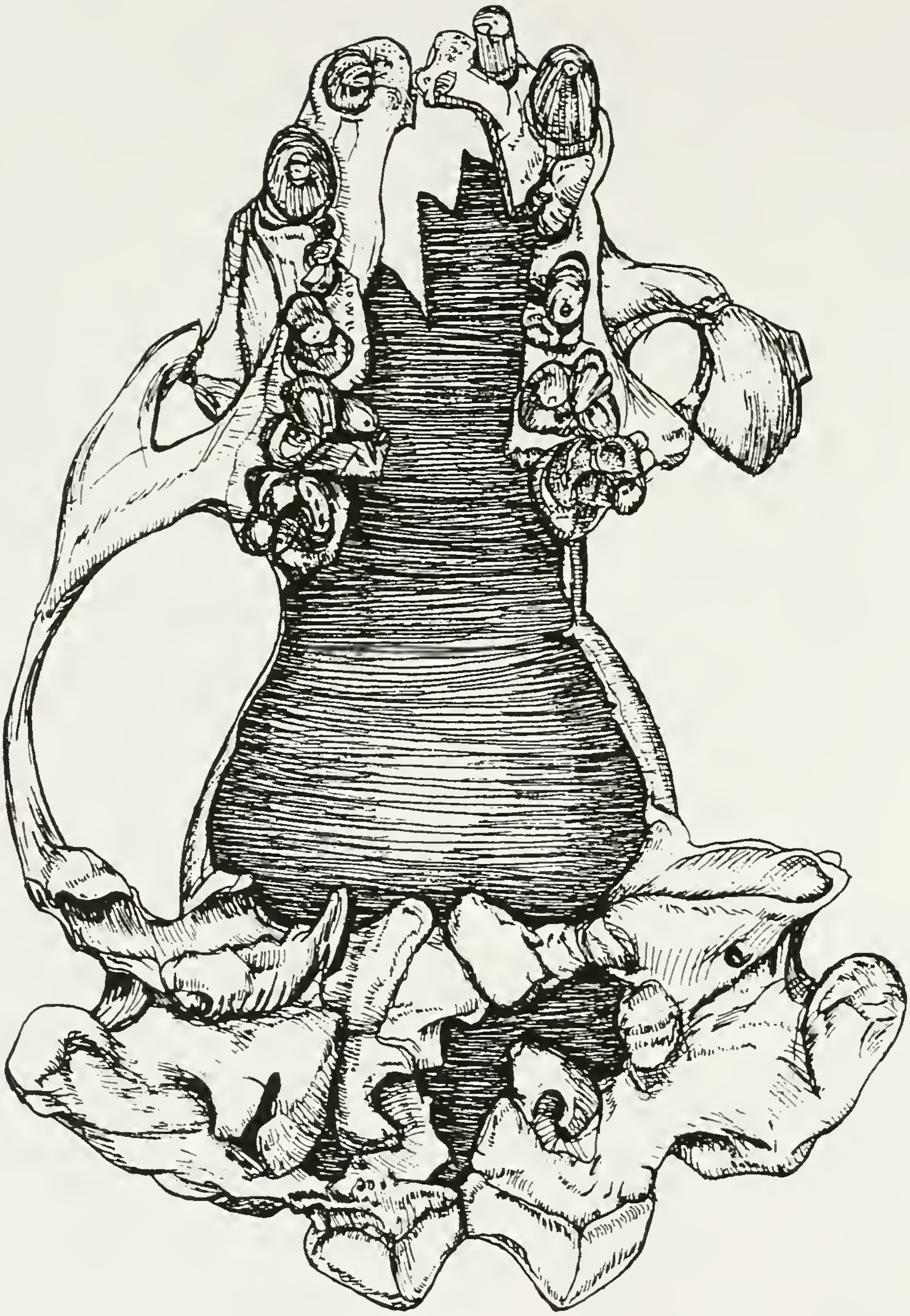


Figure 4-3. Enhydritherium skull, ventral view.

(the frontals are particularly constricted in Pteronura). Lambdoidal crests are completely absent, and the supraorbital processes are represented only by inconspicuous bumps; both of these features are known to vary ontogenetically in mustelids (Neal, 1977). The length and height of the sagittal crest is similar to that of Lutra.

In front view, the skull of this specimen resembles that of Lutra. The external nareal opening is somewhat broken, but is not greatly different from that of Lutra. All bones within the nasal region, such as the turbinals, are completely absent.

The infraorbital foramina are large but proportionate to those of Lutra and Enhydra. The premaxilla is only moderately preserved.

The ventral region of the skull is poorly preserved, with only the portion of the maxilla containing the toothrow in good condition. The medial portion of the maxilla, the pterygoids, and virtually all of the bones of the ventral floor of the braincase are absent except the floor of the right auditory bulla, which is largely intact. Relatively low and uninflated, it compares favorably with that of Enhydra and differs greatly from the thin-walled, inflated auditory bulla of Lutra. An opening into the antero-medial corner of the auditory bulla presumably is the remnant of the musculotubal canal and foramen lacerum. The bony auditory canal leading to the external meatus is directed antero-laterally with the external meatus located even with the anterior wall of the auditory bulla, a condition also observed in Enhydra, Lutra, and Amblonyx. In both Pteronura and Satherium the external meatus is even with the middle of the auditory bulla, while in Enhydriodon sivalensis the external meatus is positioned even with the posterior wall of the auditory bulla, a condition opposite to that observed in the Enhydritherium specimen (Pilgrim, 1931).

The glenoid fossae of the squamosals, including the post-glenoid walls, are essentially intact though there is some damage. As far as comparison is possible, the glenoid region resembles that of typical otters. The mastoid process is robust and distinctly elongated, contrasting the relatively short, poorly developed mastoid processes typical of mustelids. Most of the basicranial foramina in this specimen have been destroyed. The only surviving basicranial foramen on this skull, the foramen postglenoideum located immediately behind the post-glenoid wall of the glenoid fossa, resembles that of Lutra in both shape and location.

The occipital region of the skull is moderately well preserved, though a large gap is present. The occipital condyles are perfectly preserved, but show no special features. The nuchal crest is highly developed, both more robust and proportionately taller than that of any other otter. In addition, there is a deep fossa in the nuchal region that contrasts the nearly flat nuchal regions in all other observed otter skulls. This feature, in conjunction with the robust, elongated mastoid mentioned above, suggests that *Enhydritherium terraenovae* possessed neck muscles far more powerful than those of any living otter, implying the ability to forcefully turn the head and/or resist turning.(see below).

Mandible

The mandible is excellently preserved, with the only significantly breakage having occurred at the symphyseal region (Figure 4-4). The relative length of the mandible is similar to that of *Lutra*, and much greater than that of *Enhydra*. The mandible is moderately robust, more so than in *Lutra* and the other fish-eating otters but much less so than in *Enhydra*. From a dorsal view, the mandibular arcade has a typical mustelid profile. The coronoid process is broad and untapered, with a distal edge that is rounded into a symmetrical, distinctly semicircular profile. This contrasts the condition observed in the fish-eating otters, in which the coronoid process is tapered with a narrow distal edge. Like *Enhydritherium*, *Enhydra* a has broad coronoid process, though it is distinctly irregular in profile. The masseteric fossa of *Enhydritherium* is relatively deep, with its long axis oriented parallel to the toothrow and extending to a point below the anterior end of the m2, while ventrally the mandibular ramus is bordered by a large, robust shelf extending laterally. Vaguely similar masseteric fossae are also present in *Lutra*, *Pteronura*, and *Satherium*. In contrast, the mandibular fossa of *Enhydra* is extremely

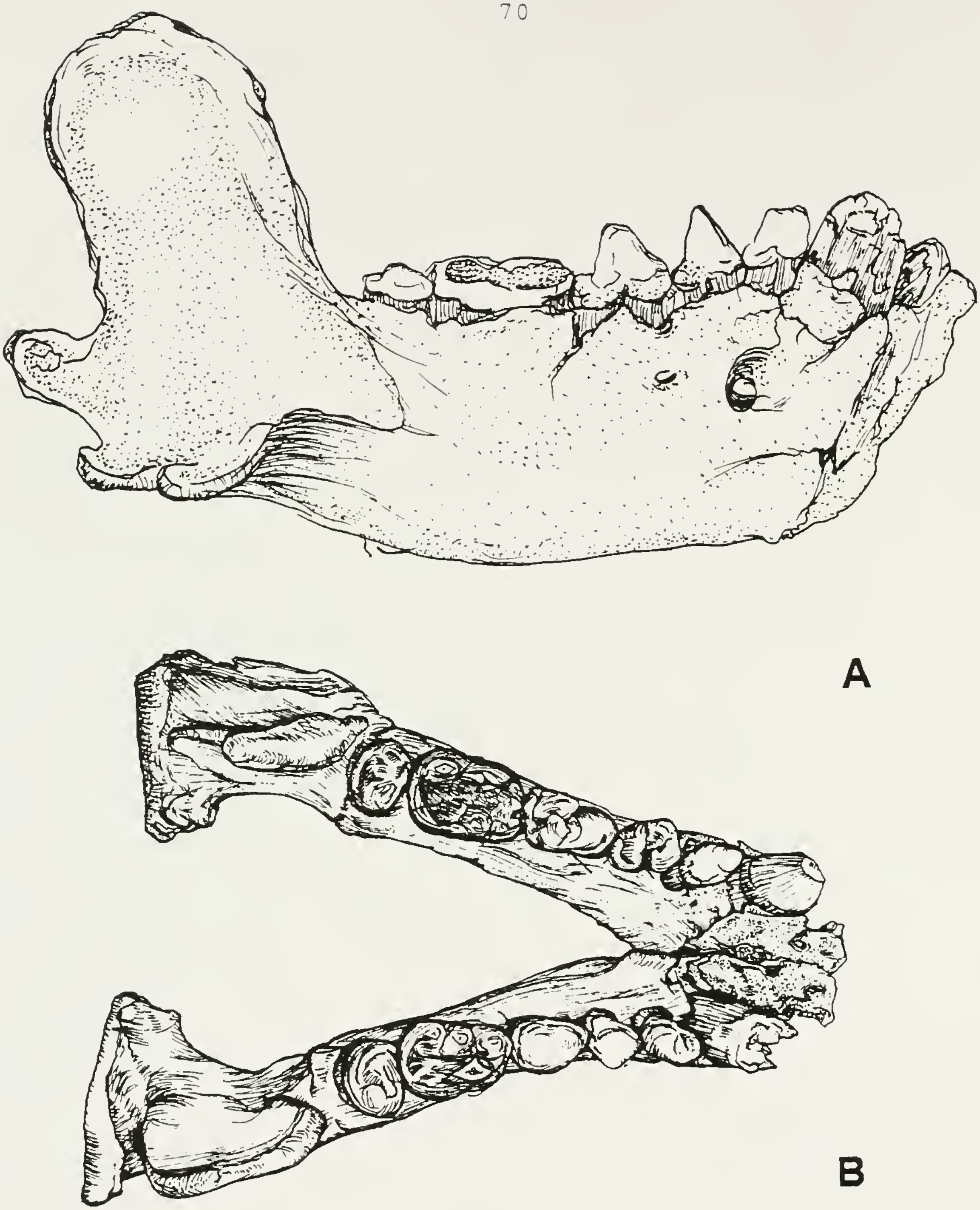


Figure 4-4. Mandible of Enhydritherium. A) lateral view; B) dorsal view.

shallow, steeply slanted relative to the toothrow, and bordered ventrally by a very small shelf on the mandibular ramus, a condition only shared with Amblonyx. (Berta and Morgan [1985] erroneously attributed a deep masseteric fossa with a distinct ventral shelf to Enhydra, considering it a synapomorphy linking Enhydra and Enhydritherium.) The mandibular condyles are well preserved, and not significantly different from those of typical otters. Measurements of the mandible are listed in Table 4-1.

Dentition

Incisors. Only the I3's are present. In their overall appearance they resemble the I3's of such extant otters as Lutra, Pteronura, and Enhydra, except in being relatively longer and more robust (see Figures 4-1 and 4-3). Pilgrim (1931) described robust I3's in Enhydriodon sivalensis.

Canines. All four canines are present in this specimen, the upper canines being well preserved and the lowers being in poor condition. The upper canines are extremely robust (see Figures 4-1 and 4-3), much more so than in any of the examined otters, a feature shared with Enhydriodon (Pilgrim, 1931). Aside from their robustness, however, they resemble the upper canines of the fish-eating otters and differ from the shorter, more slender canines of Enhydra. The lower canines of Enhydritherium are poorly preserved, with the right canine broken near the alveolus; however, the left canine retains its basic size and shape. The lower canines are much shorter than their opposing uppers, though they are similarly robust.

Premolars (excluding P4). Both the upper and lower premolars are reasonably well preserved in this specimen. Both the upper and lower premolar series range from P/p2-4 (P4 will be discussed separately below), with P/p1 absent as is typical of otters. P2 is badly fractured, though its approximate size is still discernible. It is double-rooted, and similar in size to P3 (contrasting Enhydra, in which P2 is vestigial). The P3 is reasonably intact; like P2 it is double-rooted, and posseses a distinct posterior cingulum. The lower premolars are similar in size, and all possess well developed posterior cingula (like P2, p2 is vestigial in Enhydra). The p4 of the Moss Acres Ractrack specimen differs from that of all of the examined fish-eating otters and Enhydra in lacking an accessory cusp (in Satherium two accessory cusps are present). However this absence is evidently the result of intraspecific variation; p4 accessory cusps are present on an Enhydritherium terraenovae mandible, UF 125000, recovered from the Whidden Creek Local Fauna of the Bone Valley region.

Carnassials. The carnassials (P4 and m1) of this specimen comply with the diagnosis for Enhydritherium terraenovae given by Berta and Morgan 1985), who along with with Repenning (1976) discuss the carnassial morphology of this species extensively. Thus, the carnassial morphology of this specimen will only be described briefly here. The P4 has the following features: transversely broad with a roughly quadrangular profile; paracone and metacone separate; deep valley between the paracone and protocone; hypocone rather than a hypoconal crest present; and hypocone relatively close to the protocone. The m1 is characterized by: short length with rectangular occlusal outline; large metaconid positioned opposite the protoconid; metastylid beyond the metaconid; talonid low and broad, with a shallow basin and the posterior margin squared off; and entoconid a low ridge that meets the hypoconid on the talonid ridge. The cusps are inflated relative to those of Lutra, though less so than those of Enhydra (see Figures 4-1 and 4-3, 4-14). The carnassials of this specimen are reasonably intact, though they show evidence of great masticatory wear, especially the M1. Size measurements for both the P4 and m1 are presented in Table 4-1.

Upper first molar. The M1 superficially resembles that of Lutra (see Figure 4-3). It is roughly trapezoidal in occlusal profile, with its long axis oriented labio-lingually and the lingual edge broader than the labial edge. As in Lutra, a protoloph, composed both of the protocone and paraconule, extends from the middle of the lingual edge through the interior to the middle of the anterior edge. The protoloph occludes with the posterior surfaces of the metaconid and protoconid of the m1 to form a shearing surface. The M1 differs from that of both Lutra and Enhydra in possessing a distinct hypocone. The paracone and metacone are roughly equal in size, and a small metaconule is present.

Lower second molar. The m2 of this specimen conforms in all important respects to that described for *Enhydritherium terraenovae* by Berta and Morgan (1985).

The Axial Skeleton

Except for the skull, the axial skeleton of this specimen is poorly represented. The following elements are associated with the skeleton: atlas vertebra, axis vertebra, two cervical vertebrae, four thoracic vertebrae, three lumbar vertebrae, sacrum, five caudal vertebrae, and nine indeterminate isolated vertebral centra. To the extent that comparison is actually possible, none of these specimens is significantly different from their equivalents in extant otters.

The Limbs

Both the forelimb and the hindlimb are excellently represented in this specimen, with all of the hindlimb elements represented (except possibly the fifth metatarsal) and all forelimb elements except the trapezoid. The thorough descriptions and drawings of limb elements of the *Enhydriodon* species *E. latipes* in Pilgrim (1931) allow for many of the limb elements of *Enhydritherium terraenovae* to be closely compared with those of its presumed sister genus. Limb element measurements are presented in Table 4-2.

Table 4-2. Select limb element measurements (in millimeters) of *Enhydritherium terraenovae* specimen UF 100000

Humerus	
length from head to trochlea	109
distance across epicondyles	42
Radius	
length from head to styloid process	87
Ulna	
length from olecranon to styloid process	116
Femur	
length from ball to condyle	123
distance across condyles	35
distance from ball to greater trochanter	35
Tibia	
length from proximal end to medial malleolus	125
distance across distal articulating surface	33
Fibula	
length from proximal end to medial malleolus	119

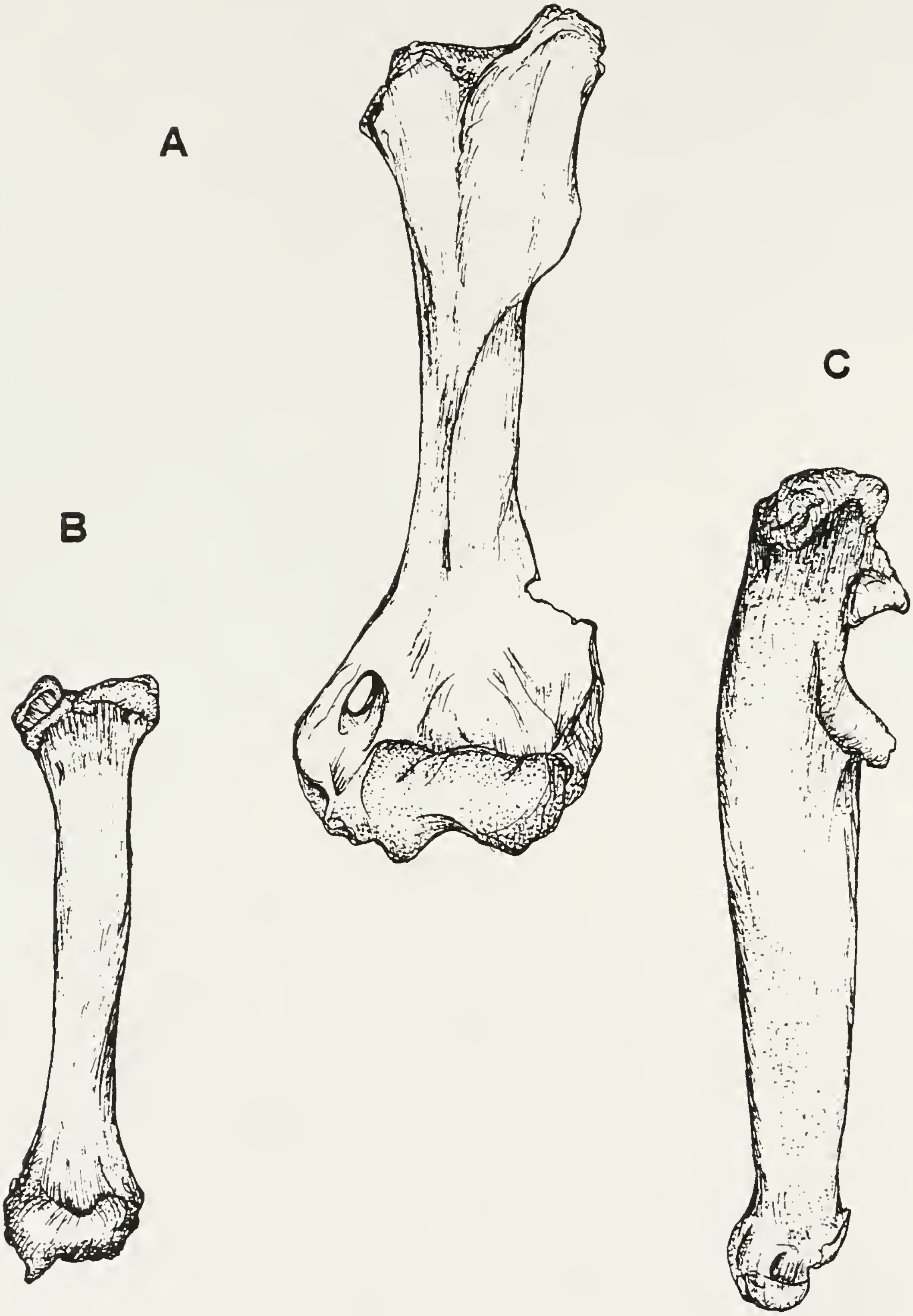
Scapula. The scapula is virtually absent from this specimen, represented only by an intact left glenoid region with a small part of the scapular spine. As far as comparison is possible, this specimen is not significantly different from the scapulae of any observed extant otters.

Humerus. The left humerus is well preserved, while the right humerus is only represented by an intact distal end (Figure 4-5). The humeral shaft is approximately equal in thickness to that of the femur, contrasting *Enhydra* in which the femoral shaft is far thicker than that of its humerus. The greater tubercle is well developed, and the deltoid and pectoral ridges are both hypertrophied and merge to form a single platelike ridge; these features features are much more poorly developed in *Lutra*, and virtually absent in *Enhydra*. The deltoid tuberosity is prominent, but is deflected laterally. A small facet separates the entepicondyle from the trochlea (the presence/absence of this facet varies considerably among otters).

Radius. Only the left radius is fully preserved; the right radius is represented only by the proximal end (Figure 4-5). It does not differ significantly from the radii of the other observed otters.

Ulna. Both the left and right ulnae are well preserved (Figure 4-5). The ulna of this specimen shows some distinct similarities to that of *Enhydra*. Like *Enhydra*, the olecronon process is reduced relative to other otters and the medial coronoid process within the olecronon fossa is absent, though

Figure 4-5. Forelimb elements of *Enhydritherium*. A) left humerus, anterior view; B) left radius, anterior view; C) right ulna, lateral view.


A
B
C

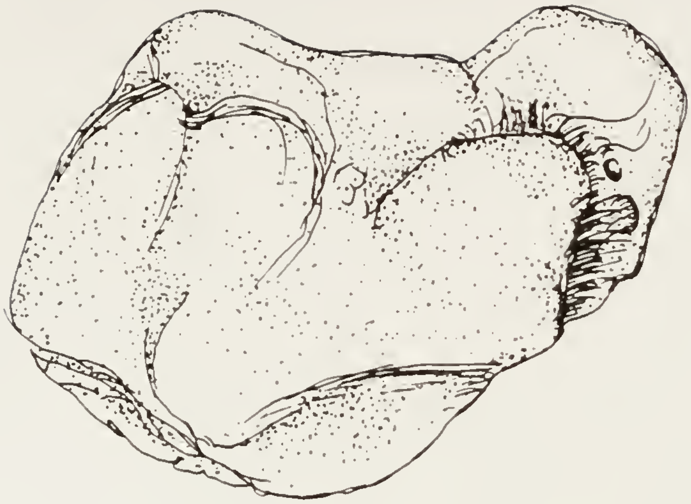
unlike *Enhydra* the coronoid process of *Enhydritherium* is replaced by a relatively large, well developed facet. The ulna is relatively deep antero-posteriorly, and the medial groove is quite shallow. The styloid process is well developed.

Scapholunar. Both left and right scapholunars are represented (Figure 4-6). The scapholunar is disproportionately large as compared to *Enhydra*, an animal roughly similar in size. The unciform facet is especially deep as compared to that of *Enhydra* and *Lutra*. However, in overall appearance it is otherwise quite similar to the scapholunars of these otters. The scapholunar of *Enhydriodon* is unknown.

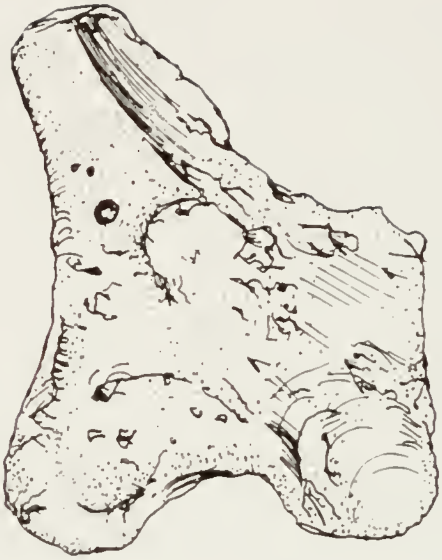
Unciform. Both left and right unciforms are present (Figure 4-6). The unciform of *Enhydritherium* is not significantly different from that of *Lutra* and *Enhydra*. The unciform of *Enhydriodon* differs greatly from that of *Enhydritherium* and other extant otters however, being tapered antero-posteriorly rather than basically oval in profile and having a posterior end that is broader than the anterior end, with a distinct medial constriction.

Magnum. Only the left magnum is represented (Figure 4-6). The lateral portion is missing, so a detailed comparison with the magna of other otter taxa is impossible. The surviving portion closely resembles the magnum of *Lutra*. The magnum of *Enhydriodon* is unknown.

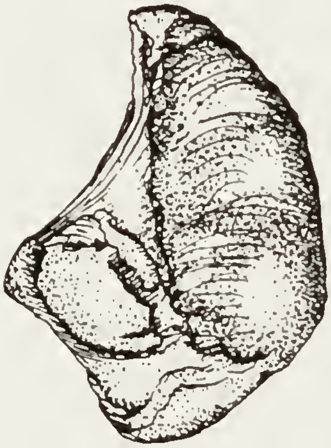
Figure 4-6. Carpal elements of *Enhydritherium*. A) left scapholunar, anterior view; B) left magnum, posterior view; C) right cuneiform, posterior view; D) right cuneiform, anterior view; E) right trapezius, dorsal view; F. left unciform, posterior view.



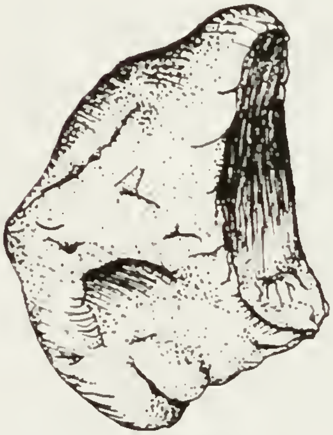
A



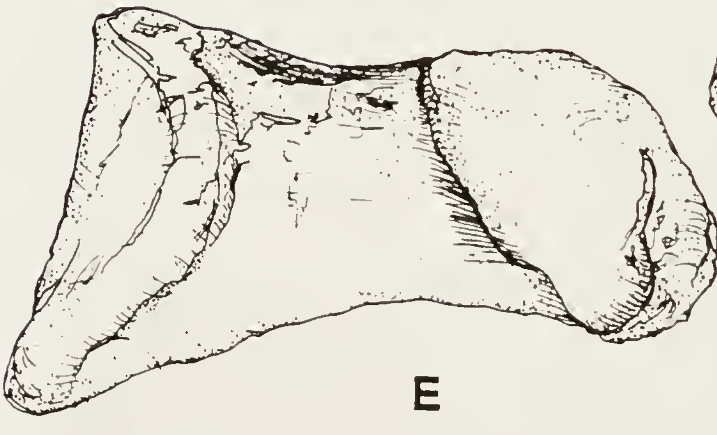
B



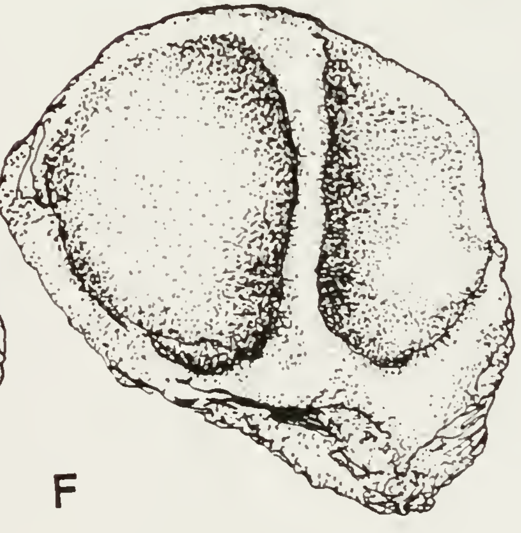
C



D



E



F

Cuneiform. Both left and right cuneiforms are represented (Figure 4-6). This cuneiform is very similar to that of both *Lutra* and *Enhydra*. The cuneiform of *Enhydriodon* is unknown.

Trapezius. Only the right trapezius is present (Figure 4-6). It does not differ significantly from the trapezius of *Enhydra*, while the trapezius of *Enhydriodon* is not adequately pictured in Pilgrim (1931) to allow a comparison.

Metacarpals. Six metacarpals are preserved, including left I, right II, left III, right IV, and left and right V; metacarpal III is pictured in Figure 4-7. Their morphology is similar to that of *Enhydriodon*, and their proportions similar to those of *Lutra*. In contrast, the metacarpals of *Enhydra* are extremely short, almost stumpy in comparison.

Pelvis. The pelvis is present, but is far too poorly preserved to allow any comparisons with the pelves of other otters.

Femur. Only the left femur is represented. The femur of this specimen is not significantly different from the femora of the observed fish-eating otters beyond its greater size (Figure 4-8). However, the femur of *Enhydra* differs greatly from all of the femora of the other otters examined, including *Enhydritherium*, in being highly robust and short relative to the humerus, having greatly enlarged trochanters, and having a hypertrophied medial condyle.

Tibia. Only the left tibia is present. This tibia agrees closely with the tibia of *Enhydritherium terraenovae*

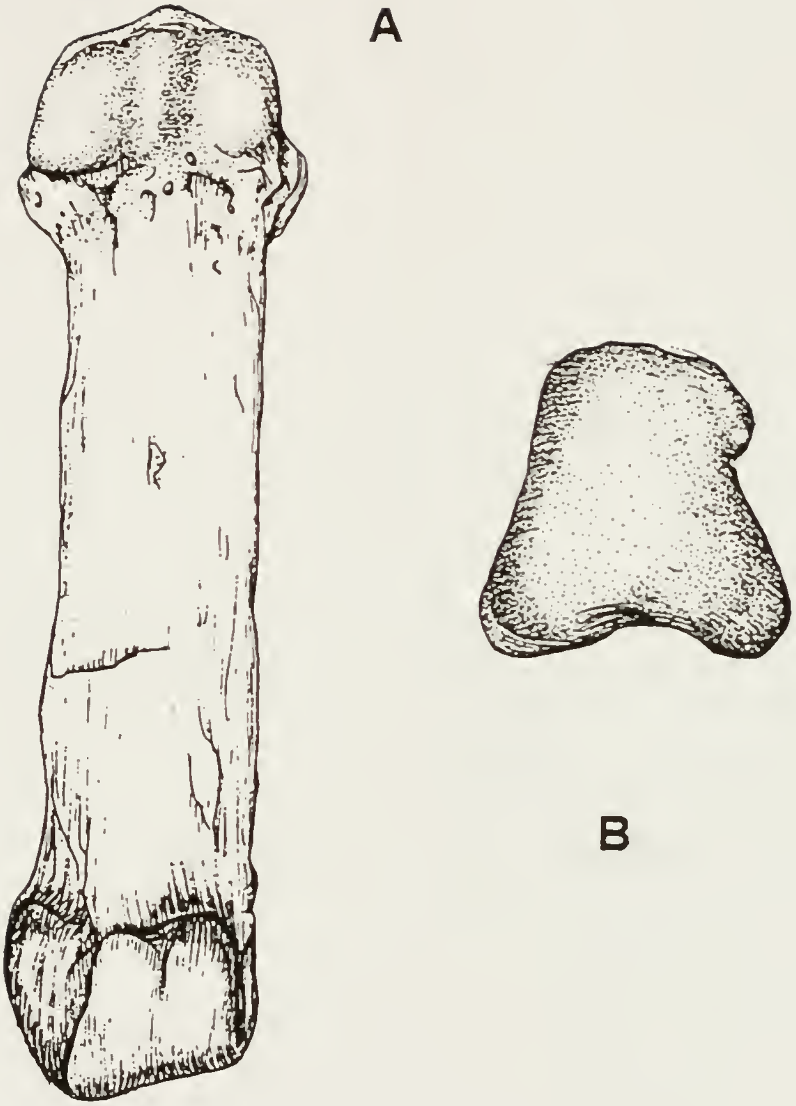


Figure 4-7. Close-up of *Enhydritherium* left metacarpal III. A) dorsal view; B) proximal articulation surface.

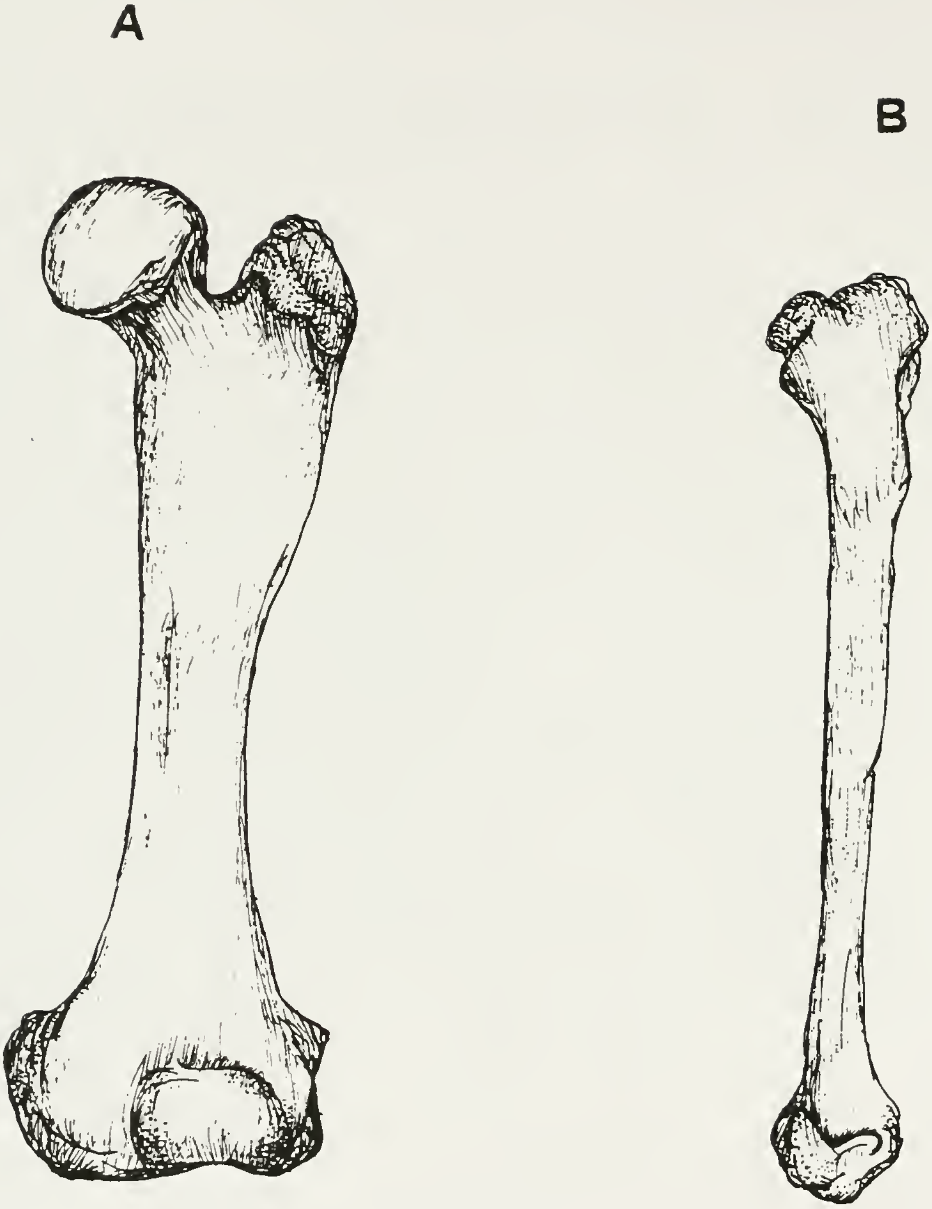


Figure 4-8. Enhydritherium hindlimb elements. A) left femur, anterior view; B) left fibula, anterior view.

described in Berta and Morgan (1985), though it is considerably smaller than the described specimen. It differs from the tibiae of all other observed otters in having a greatly reduced medial malleolus and a poorly developed tibial crest.

Fibula. Only the left fibula is represented (Figure 4-8). This specimen differs from the fibulae of all of the other examined otters in being unflattened and relatively robust. In addition, it has poorly developed crests for muscle attatchment, and an extra process adjacent to its lateral malleolus absent from the other observed otters.

Astragalus. Both the left and right astragali are preserved (Figure 4-9). The astragalus of this specimen is disproportionately small relative to those of other otters. The neck is distinctly abbreviated (this feature varies considerably among the otters, Enhydriodon for example having a relatively elongated neck). In all other respects the astragalus of Enhydritherium resembles that of the other observed otters.

Calcaneum. Both the right and left calcanei are preserved (Figure 4-10). However, the right calcaneum shows coarse extra growth indicating a pathological condition in the right ankle of the animal. This condition appears in many of the right tarsals of this specimen and thus, when possible, only the left tarsals are used for comparative purposes. The calcaneum is characterized by a distinct slenderness with little expansion at the distal end of the

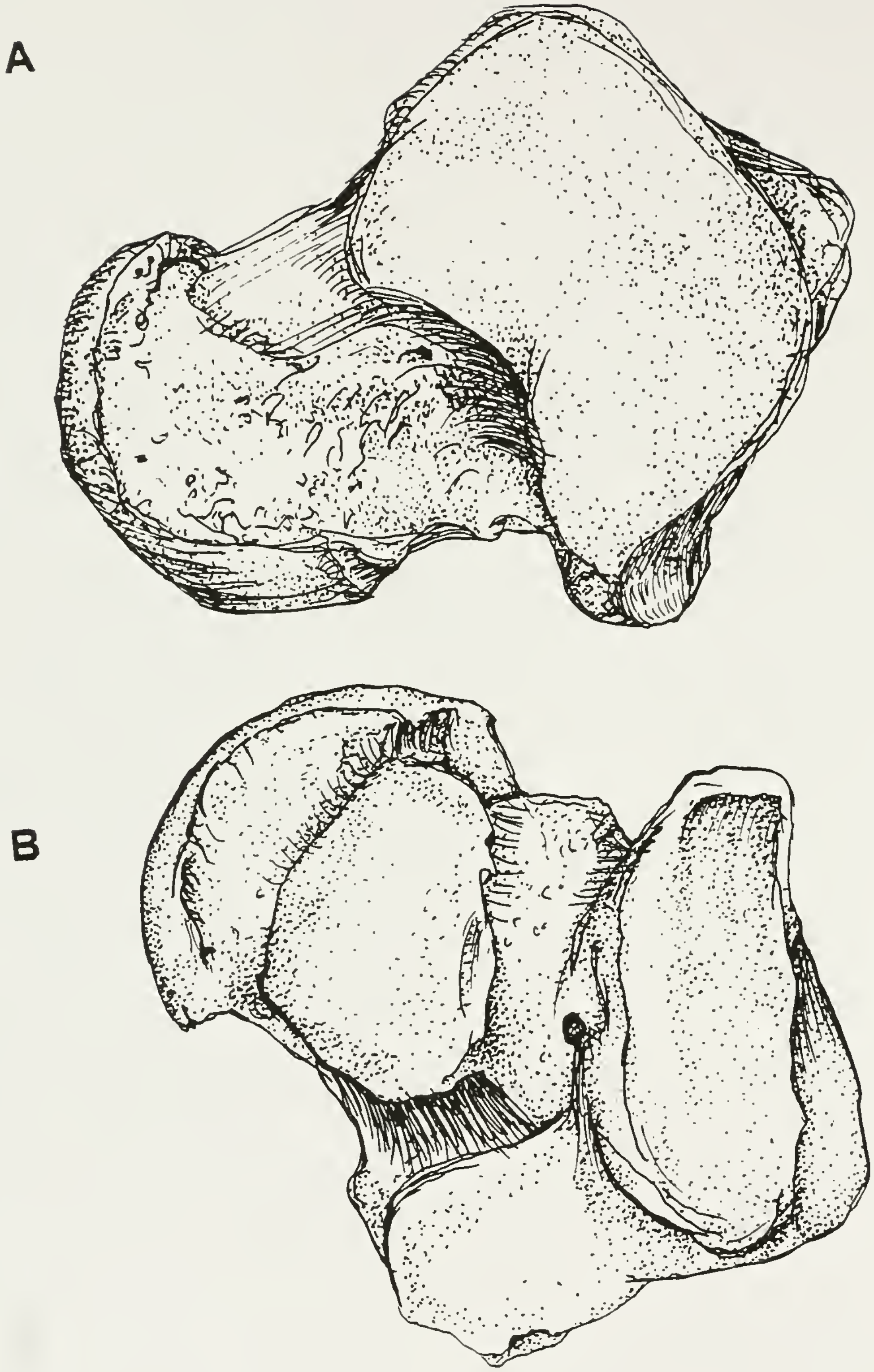


Figure 4-9. Left astragalus of *Enhydritherium*. A) dorsal view; B) ventral view.

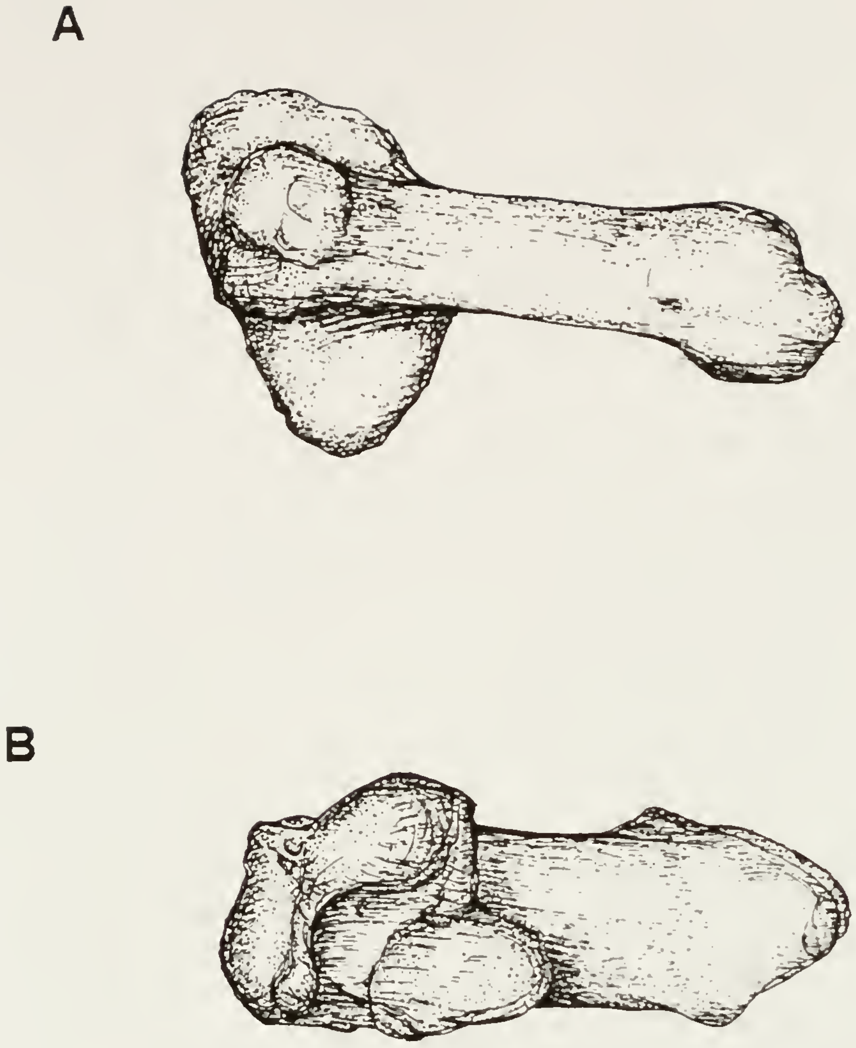


Figure 4-10. Left calcaneum of *Enhydritherium*. A) ventral view; B) dorsal view.

tuber, a condition contrasting all the other otters observed including Enhydriodon. A trait shared with Enhydriodon, but absent from the other otters, is the absence of the latero-anterior astragalar articulating facet on the dorsal surface.

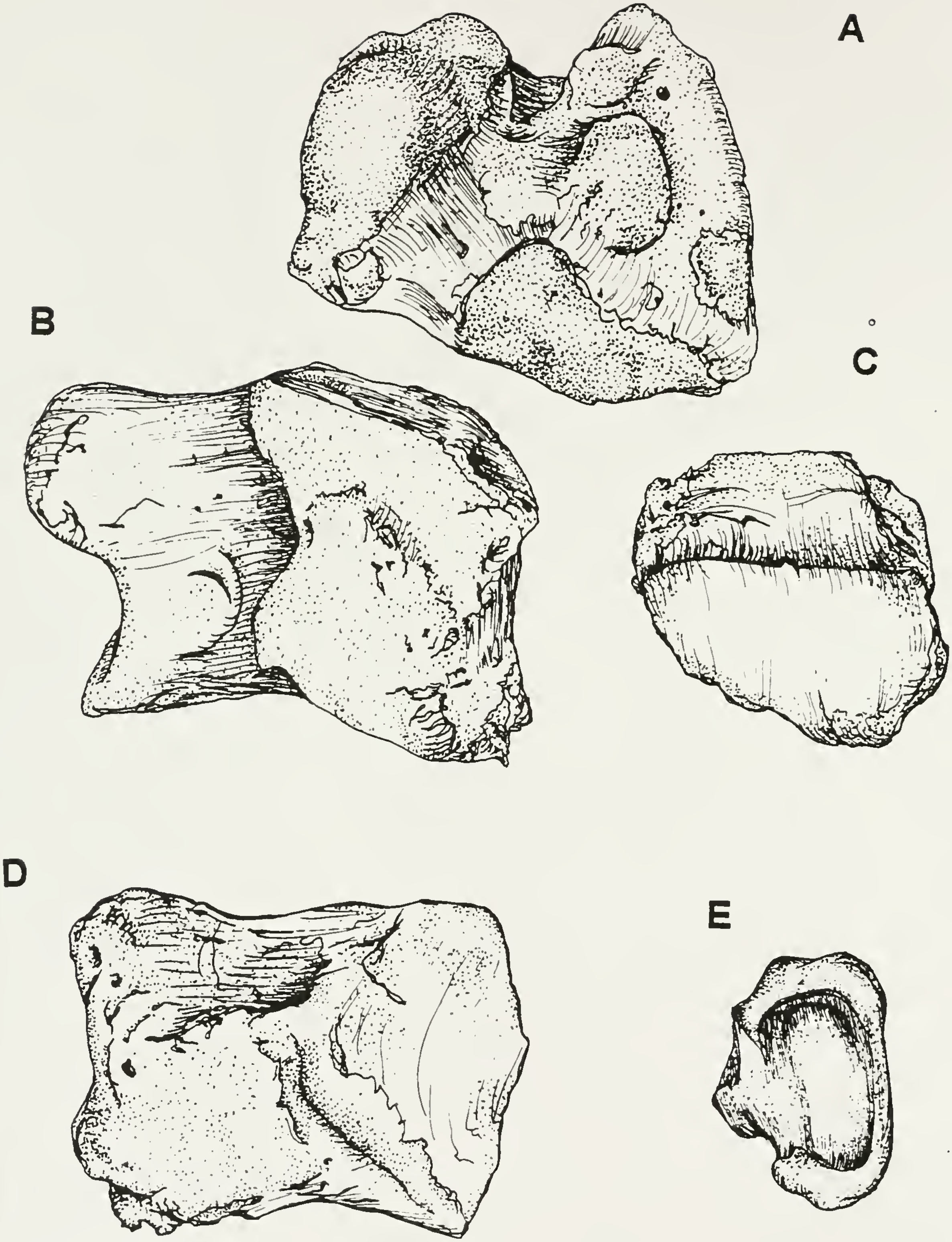
Cuboid. Both the right and left cuboids are present (Figure 4-11). The cuboid is very similar to that of Enhydriodon except that it possesses an extra process on the ventral surface for articulating with the calcaneum. The overall resemblance to Lutra is very close.

Navicular. Both the left and right naviculars are present (Figure 4-11). Compared to Enhydriodon, the navicular of this specimen is more slender, and there is a prominent process on the antero-medial edge absent from Enhydriodon.

Ectocuneiform. Both the left and right ectocuneiforms are preserved (Figure 4-11). The ectocuneiform of this specimen is almost identical to that of Enhydriodon, with the one difference being a small process on the dorsomedial surface. The ectocuneiforms of both taxa broadly resemble those of Lutra and Enhydra.

Mesocuneiform. Both the left and right mesocuneiforms are present (Figure 4-11). The mesocuneiforms of Enhydritherium and Enhydriodon are virtually identical, which in turn are almost identical to that of Lutra. Enhydra differs from all of the above otters in having a relatively slender mesocuneiform.

Figure 4-11. Tarsal elements of *Enhydritherium*. A) left cuboid, anterior view; B) left ectocuneiform, anterior view; C) left mesocuneiform, anterior view; D) right entocuneiform, posterior view; E) left navicular, posterior view.


A
B
C
D
E

Entocuneiform. Only the right entocuniform is preserved (Figure 4-11). Exstensive pathological growth is present, making detailed comparison with other otter entocuneiforms difficult. However, in overall shape it closely resembles the entocuneiforms of Enhydriodon and Lutra, and differs from Enhydra in being considerably less robust.

Metatarsals. Eight metatarsals are preserved, consisting of left and right I, left and right II, left and right III, and left and right IV; metatarsal III is shown in Figure 4-12. Metatarsal V is absent, and it is unknown whether this is due to a failure in preservation or true absence. The complete representation of all of the other metatarsals lends considerable weight to the latter possibility. If indeed metatarsal V is absent from Enhydritherium, then this represents a considerable deviation from the normal mustelid condition. The metatarsals of Enhydritherium and Enhydriodon are essentially identical, and both differ from those of all other otters (and terrestrial carnivorans in general) in being short and slender, little longer than the metacarpals. The contrast is greatest with Enhydra, whose metatarsals are grossly elongated and flattened as a swimming adaptation, particularly metarsal V (see below).

Phalanges. A total of twenty-two phalanges are preserved, represented by nine proximal, seven medial, and six distal phalanges (Figure 4-13). The phalanges of the manus and pes are indistinguishible (assuming that phalanges

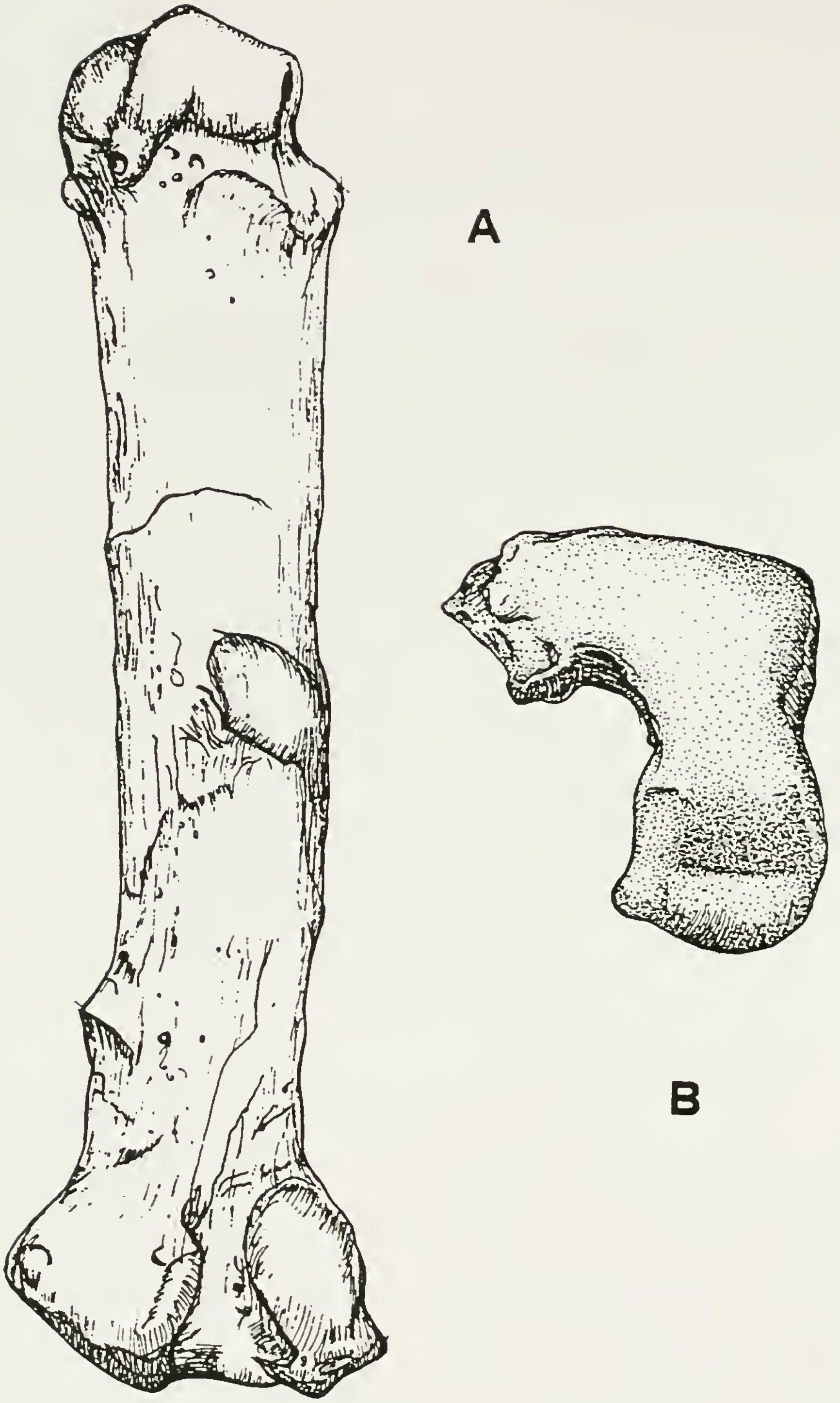


Figure 4-12. Close-up of Enhydritherium left metatarsal III. A) dorsal view; B) proximal articulating surface.

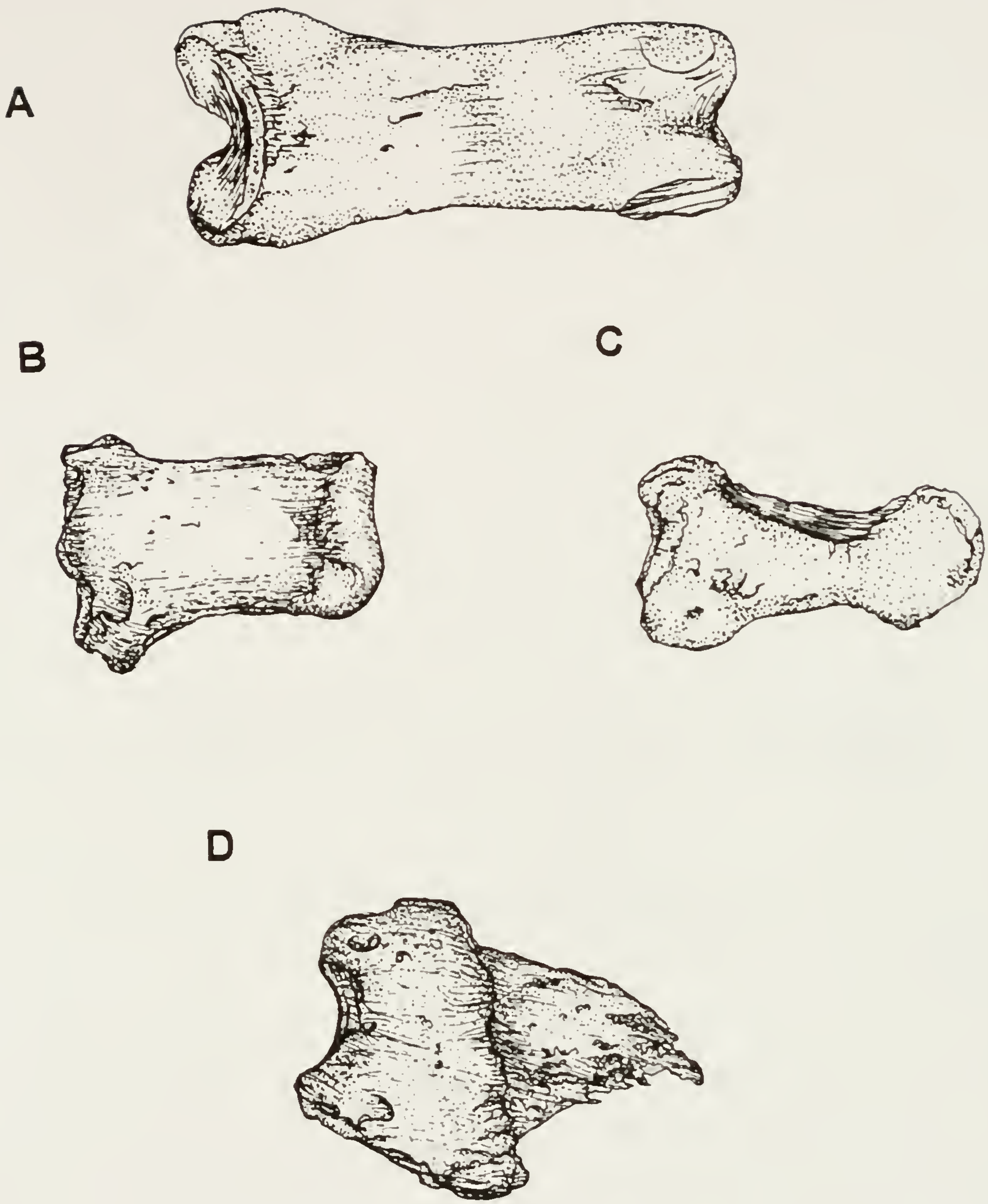


Figure 4-13. Phalanges of Enhydritherium. A) proximal phalanx, dorsal view; B) medial phalanx, dorsal view; C) medial phalanx, lateral view; D) ungual phalanx, lateral view.

from both regions have been recovered). The preservation ranges from excellent to poor. The proximal and medial phalanges of this specimen resemble in overall morphology those of *Enhydriodon* and typical otters as a whole. However, the distal phalanges differ from those of the other observed otters in having extremely large ungual sheaths, indicating the presence of exceptionally large claws.

The medial phalanges of *Enhydritherium* have features that warrant special consideration. The medial phalanges of this specimen have distinct depressions on their dorsal surfaces that extend most of the length of their shafts, with small but distinct tuberosities at their proximal borders. A similar condition is found in *Enhydriodon*; however, in *Enhydriodon* the depression is shallower, extends only two-thirds the length of the shaft, and is displaced laterally towards the internal surface, while the shaft as a whole is distinctly curved medially. Pilgrim (1931) interpretted this condition in *Enhydriodon* as indicating the presence of retractile claws, based in part on a somewhat similar condition found in most cats; the medial shaft curvature (absent from *Enhydritherium*) provides a potential space for the retracted distal phalanx to reside when retracted. *Enhydra* is also known to possesses retractile claws (Mason and Macdonald, 1986). However, its medial phalanx differs from that of felids, *Enhydritherium*, and *Enhydriodon* in lacking a dorsal fossa and a medial curvature of the shaft, though the proximal tuberosity is well developed. This same pattern is seen in the procyonid Bassariscus astutus, another carnivoran known to have retractile claws (Nowak and Paradiso, 1983). The variation in medial phalanx morphology in living carnivorans with retractile claws makes exact evaluation of the condition seen in Enhydritherium difficult, though claw retractility is a plausible interpretation.

Rediagnosis of Enhydritherium terraenovae

The original diagnosis of Enhydritherium terraenovae by Berta and Morgan (1985) was based on limited material, mainly carnassials and fragmentary mandibular material. The partial skeleton of Enhydritherium terraenovae represented by the Moss Acres Racetrack specimen allows for the diagnosis of this genus and species to be expanded so as to include extensive cranio-mandibular and postcranial characters. Since the genus is currently monospecific, the diagnosis is the same for both the genus and species.

The rediagnosis is as follows. Lutrine of large size, similar to that of Enhydra. Lower canines greatly reduced relative to the upper canines; p2 double rooted; P4 highly triangular and transversely broad, with a posteriorly positioned protocone, large separation of paracone and protocone with a deep valley between them, and protocone positioned close to the hypocone; m1 lacking a continuous buccal cingulum, with exceptionally inflated cusps and broad talonid; m2 with ovoid outline. Tall triangular process present on the dorsal surface of the jugal; temporal crest absent; supraorbital process virtually absent; mastoid process elongated; nuchal crest tall and robust, with a deep posteriorly directed fossa; coronoid process with a semicircular distal profile. Humeral pectoral and deltoid ridges hypertrophied; coronoid process in the olecranon fossa absent, replaced by a well developed facet; medial malleolus and tibial crest of the tibia highly reduced; fibula relatively unflattened and robust; calcaneum slender, with a narrow tuber; navicular slender, with a prominent process on the antero-medial edge; medial phalanx with a deep dorsal depression extending most of the length of the shaft; distal phalanx with a large ungual sheath.

Paleoecology and Functional Morphology

Habitat

Prior to the discovery of the Moss Acres specimen, Enhydritherium terraenovae fossils were known from the following depositional environments: (1) nearshore marine with terrestrial mammals rare (all California sites including the San Joaquin and San Mateo Formations); (2) fluvio-deltaic, with both a strong marine and terrestrial mammal fauna (the Bone Valley Formation of Central Florida); and (3) lacustrine, dominated by a terrestrial mammal fauna with both a typically freshwater herpetofauna including amphibians, and a small euryhaline marine ichthyofauna (the Withlacoochee River 4A site) (Berta and Morgan, 1985). Berta and Morgan (1985) interpreted these depositional environments as indicating a strong preference by Enhydritherium terraenovae for marine and marine-associated environments, and explained its absence from the well known continental interior Hemphillian and Blancan faunas on this basis.

The discovery of the Enhydritherium terraenovae specimen at the Moss Acres Racetrack site does not contradict the interpretation of Berta and Morgan regarding the habitat preference of this animal outright. However, it does suggest a need for its modification. The Moss Acres Racetrack site represents an inland lacustrine environment, probably an isolated pond or small lake formed in a sinkhole, with no trace of a marine fauna beyond a few shark teeth reworked from the surrounding limestone. The terrestrial mammal fauna suggests an adjacent savanna open woodland habitat (see chapter 9). The sea level at the time of deposition is unknown, but the coast was surely several kilometers away from the site (currently the site is approximately seventy kilometers from the nearest coastline). This is clearly an unlikely habitat in which to find an animal strongly bound to the sea.

The evidence for an association between Enhydritherium and marine environments is indisputable. However, the presence of Enhydritherium at the Moss Acres Racetrack site and to a lesser extent the Withlacoochee River 4A site suggests that this animal was not specialized for a marine existence to the same degree as modern Enhydra. Rather, it appears to have been a habitat generalist, capable of living in both nearshore marine and inland fresh water environments. The presence of Enhydritherium at Moss Acres, which was a number of kilometers from the coast (though perhaps closer to one or more coastal rivers), further suggests that this animal had the locomotive capacity to traverse a significant distance overland (a capacity lacking in Enhydra, though present in Pteronura despite a degree of clumsiness [Nowak and Paradiso, 1983; see below]). However, it is interesting that all of the sites from which Enhydritherium has been found are in fairly close proximity to the coast, certainly within one hundred kilometers. Thus Enhydritherium was apparently bound to coastal regions if not the coast itself, though the basis for this connection is unclear. This connection, whatever its nature, may have prevented Enhydritherium from entering the Mio-Pliocene mid-continental faunas of North America as suggested by Berta and Morgan.

Locomotion

It is possible on the basis of limb morphology to make inferences about an animal's mode of locomotion, and thus to an extent its prefered habitat (e.g. aquatic versus terrestrial). The preservation and completeness of the limb elements of the Moss Acres Racetrack Enhydritherium terraenovae specimen allow this aspect of this animal's autecology to be examined for the first time.

As discussed above, the limb elements of Enhydritherium differ greatly from Enhydra and roughly resemble those of

Lutra. The major differences between *Enhydritherium* and *Enhydra* are summarized as follows. (1) The humeral and femoral shafts of *Enhydritherium* are of roughly equal robustness, while in *Enhydra* the femoral shaft is considerably more robust than that of the humerus. (2) The humerus of *Enhydritherium* has a relatively large greater tubercle and hypertrophied pectoral and deltoid ridges, contrasting *Enhydra* in which both the greater tubercle and pectoral ridge are extremely small or absent. (3) The metacarpals of *Enhydritherium* are similar in proportion to those of most other otters, while in *Enhydra* they are highly shortened relative to the metatarsals. (4) The post-femoral elements of *Enhydritherium*, in direct contrast to *Enhydra*, are either poorly developed (e.g. the tibia) or show no particular evidence for specialized usage in swimming (e.g. the metatarsals are not elongated or flattened).

The short metacarpals, relatively weak humeral muscles as indicated by the poorly developed muscle insertion surfaces on the humerus, robust femur, and highly elongated distal hindlimb elements found in *Enhydra* all suggest that this animal is specialized for propelling itself with its hindlimbs, an interpretation verified by observation of living sea otters (Mason and Macdonald, 1986; Tarasoff et al., 1972). The hands, with their shortened digits, are used primarily for food manipulation, and are kept close to the body during swimming. Since *Enhydra* rarely comes far onto land, seldom going more than 75 meters from the shore, effective terrestrial locomotion is not crucial to the animal (Kenyon, 1975).

The poorly developed or unspecializied (in a swimming context) distal hindlimb elements and heavily developed humeral muscles of Enhydritherium strongly suggest that, contrary to Enhydra, this animal was primarily a forelimb swimmer. This interpretation is reinforced by the specific humeral muscles that were apparently hypertrophied, the latissumus dorsi (greater tubercle insertion), pectoral complex, and deltoid complex (delto-pectoral ridge insertion) muscles all being crucial for humeral retraction, adduction, and abduction during forelimb swimming (Webb and Blake, 1985). The hypothesis that Enhydritherium was specialized as a forelimb swimmer is further supported by a strong overall similarity between the humerus of Enhydritherium and that of a known extant forelimb swimmer, the otariid seal Zalophus californianus (Allen, 1880; Bonner, 1984; Nowak and Paradiso, 1983). Like Enhydritherium, the humerus of Zalophus has both a highly enlarged greater tubercle and an enormous delto-pectoral ridge (the two ridges being enlarged to such an extent that they have fused into a single thick, block-like structure).

The living fish-eating otters lie between Enhydritherium and Enhydra in their mode of swimming, utilizing both their fore- and hindlimbs. However, there is a tendency for the hindlimbs to dominate over the forelimbs (Rosevear, 1974; Tarasoff et al., 1972; Estes, 1989). In addition, the living fish-eating otters as well as Enhydra utilize carangiform caudal undulations to an extent for propulsion (Tarasoff et al., 1972). Such caudal undulation may have had a role in the swimming of Enhydritherium as well; however, the caudal region of the vertebral column is inadequately known to address this question.

With its more balanced forelimb/hindlimb proportions, Enhydritherium was almost certainly more competent for terrestrial locomotion than Enhydra. Living fish-eating otters, which have superficially similar limb proportions, despite their aquatic propensities tend to spend considerable amounts of time on land and may cross long distances. This is in great contrast to Enhydra, which seldom if ever moves far from shore (Rosevear, 1974; Taylor, 1989; Kenyon, 1975). In evaluating cursoriality and thus in a crude sense terrestrial locomotive effectiveness of carnivores, one of the most useful indices is the metapodial/propodial length ratio (Taylor, 1989). These data for Enhydritherium, Enhydra, Lutra, and Mustela are presented in Table 4-3, with the third digit chosen to represent the metapodials. In this data set Lutra and Mustela are almost indistinguishible, evidently reflecting the known terrestrial competence of Lutra. Both Enhydritherium and Enhydra differ significantly from Mustela and Lutra, though in different ways. The strong restriction of Enhydra to an aquatic environment is reflected in its propodial/metapodial length ratios. The metacarpals are drastically shortened relative to their corresponding

Table 4-3. Measurements of propodial and metapodial element lengths (millimeters) and their ratios for _Enhydritherium_, _Enhydra_, _Lutra_, and _Mustela_.

Element	E	Eh	L	M
ulna	102	122	63	32
metcarpal III	32	27	26	14
ulna/metacarpal III	3.2	4.5	2.4	2.3
tibia	125	152	91	45
metatarsal III	42	71	39	19
tibia/ metatarsal III	3.0	2.1	2.3	2.4

abbreviations: E= _Enhydritherium_, Eh= _Enhydra_, L= _Lutra_, M= _Mustela_.

propodials, showing a ratio much larger than that shown by any of the other examined taxa. In addition the metatarsals are highly elongated, again significantly more so than in any of the other observed taxa.

Like *Lutra* and *Mustela* and unlike *Enhydra*, *Enhydritherium* has equally proportioned fore- and hindlimbs. However, *Enhydritherium* differs from the aforementioned taxa in having metapodials that are consistently short relative to the propodials, or conversely propodials that are elongated relative to the metapodials. This feature suggests that *Enhydritherium* was less competent at terrestrial locomotion than *Lutra* (though not necessarily incompetent) and by implication more specialized for swimming, though less so than *Enhydra*.

Diet

The bunodont otters (here considered to be a phenetic rather than a strictly phylogenetic group), as suggested by their monicker "the crab-eating otters," are generally assumed to be as a whole specialized for hard foods such as crabs and other arthropods. The diet of the one extant bunodont otter, *Enhydra*, consists primarily of such hard foods as crabs, sea urchins, gastropods and bivalves. However, relatively soft foods such as fish and cephalopods are also commonly consumed by *Enhydra*, and in some populations these soft items may be more important than hard ones (Mason and Macdonald, 1986; Kenyon, 1975). The consumption of these hard food items (particularly the bivalves) as well as the accidental consumption of significant amounts of sand causes an enormous amount of wear on the carnassial cusps of this animal, despite their extreme thickness. Though they have relatively slender carnassial cusps, fish-eating otters may consume significant quantities of hard food items as well; for example, crabs constitute a major part of the diet of the African clawless otter Aonyx capensis. Other fish-eating otters may also consume considerable quantities of such hard items as molluscs and crayfish (Rosevear, 1974).

The thickened cusps of Enhydritherium terraenovae carnassials and their tendency to be heavily worn suggest that these otters, like Enhydra, consumed extremely hard food items such as molluscs (arthropods are specifically excluded from this category, since their chitinous exoskeletons can be opened by slicing as well as crushing). Both direct and indirect evidence, however, indicates that at least under certain circumstances this animal subsisted mainly on relatively soft foods. Matrix from the jacket in which the Moss Acres Racetrack specimen was collected yielded a significant amount of fish bone during screenwashing, an extremely rare fossil in the site. This local concentration of fish material around the otter can be plausibly explained as stomach contents, thus suggesting that Enhydritherium fed on other items than the hard foods indicated by its worn bunodont teeth. Biogeography provides indirect evidence that

Enhydritherium abandoned durophagy at times. *Enhydritherium* is known from at least two aquatic inland sites that had little or no contact with the sea, the Withlacoochee 4A and Moss Acres Racetrack. The aquatic mollusc fauna in Florida during the Miocene was dominated by relatively small species (i.e. mostly less than three centimeters in diameter) such as the gastropods common in the modern Florida faunas. Unionid clams, the only modern aquatic molluscs in Florida that typically reach the large sizes commonly attained by marine molluscs, were extremely rare or completely absent from Florida during the Miocene, and did not become common in this region until the Pleistocene (Portell, pers. comm.). At the very least *Enhydritherium* was similar in size to, if not on average larger than, *Enhydra*, which usually ranges from 22 to 45 kilograms for adult males (Nowak and Paradiso, 1983). (On the basis of a calculation involving combined humeral and femoral minimum shaft circumferences as discussed in Alexander [1989], the body mass of the Moss Acres Racetrack *Enhydritherium* individual has been estimated at approximately 22 kilograms; see chapter 9.) It is unlikely that an animal of this size could have sustained itself on such small food parcels. Therefore, it would appear that when in aquatic habitats *Enhydritherium* largely abandoned a mollusc diet in favor of such relatively large food parcels as fish and arthropods (e.g. crayfish) in order to satisfy its appetite. Indeed, as occasionally observed in *Enhydra* individuals and populations, *Enhydritherium* may have had a dual diet in marine environments.

Finally, morphological evidence suggests that *Enhydritherium* as a whole may have much more dependent on fish than living *Enhydra*. As has already been discussed, the forelimb elements of *Enhydra* are smaller and/or more poorly developed than is normal for all other otters, particularly in the metacarpals. This feature is reflected in the foraging patterns and diet of *Enhydra*. *Enhydra* uses its forelimbs extensively to manipulate prey, in contrast to the living piscivorous fish-eating otters that rely exclusively upon their mouths for this purpose. This reliance on its forelimbs, particularly its manus, requires *Enhydra* to have great manual dexterity and sensitivity, which precludes the extensive development of its forelimbs for locomotion (this same pattern is also observed in the invertebrativorous otter *Aonyx capensis*). Estes (1989) proposed that this reliance on manual prey apprehension is the basis for the evolution of the extremely specialized hindlimb swimming in *Enhydra*. *Enhydritherium*, in contrast, is characterized by metacarpals of ordinary otter proportions and a forelimb highly developed for swimming, implying that like the living piscivorous otters it relied upon its mouth for apprehending its prey rather than its hands. This situation strongly suggests that *Enhydritherium* was far less specialized for eating invertebrates than *Enhydra*; indeed, were it not for their heavily worn bunodont carnassials, there would be no basis for believing that *Enhydritherium* ate anything other than fish.

Finally, on a highly speculative note, it should be noted that *Enhydritherium* apparently had very powerful neck muscles as indicated by its large, elongated mastoid process and high, thick nuchal crest. These features make little sense in the context of invertebrate feeding. If however *Enhydritherium* habitually caught particularly large fish with its mouth, powerful neck muscles could conceivably have helped it handle the strong, thrashing prey.

Phylogeny

The phylogenetic relationship of the extinct bunodont otters to *Enhydra* has been subject to dispute, with some advocating a close relationship between them and others rejecting any relationship, though recent literature (e.g. Repenning, 1976; Hendey, 1978) has favored an *Enhydra* descent from one of the extinct bunodont otters. The one obvious character shared by *Enhydra*, *Enhydritherium*, and *Enhydriodon* is bunodonty. This character by itself is insufficient to conclusively support the monophyly of these taxa relative to the other otters however, since bunodonty would be a likely convergence if separate otter lineages independently undertook a durophagous diet. Other features, less prone to convergence under the influence of durophagy, must be examined to strengthen the hypothesis of bunodont otter monophyly.

The distribution of key cranial, dental, and post-cranial characters among *Enhydritherium*, *Enhydriodon*, *Enhydra*, *Lutra*, and *Mustela* (a non-lutrine mustelid outgroup) is presented in Table 4-4 (no characters are presented that varied significantly within the fish-eating otters to reduce phylogenetic "noise"). This character matrix was not subjected to an analysis with the Phylogenetic Analysis Using Parsimony (PAUP) program because the small number of useful (i.e., non-autapomorphic or symplesiomorphic) characters rendered a direct analysis sufficient for the task at hand. A close relationship (possibly sister taxa-see below) between *Enhydritherium* and *Enhydriodon* is indicated by the following shared features: 1) a dorsally grooved medial phalanx, 2) short metatarsals, and 3) hypocone on the P4 and M1, a feature not found in any fish-eating otters and rare in mustelids in general (a hypocone is present in the Old World badger *Meles*) (see Table 4-4). The status of the hypocone of *Enhydra* is disputed. Traditionally the hypocone is considered to be absent from *Enhydra*, and it has been proposed on this basis that the bunodont condition in *Enhydritherium*/*Enhydriodon* and *Enhydra* is the result of parallelism (Repenning, 1976) (Figure 4-14). Repenning (1976) however proposed that *Enhydra* indeed has a hypocone but that it has been misdiagnosed as the protocone, the true protocone having been secondarily lost. He based this proposal on the basis of the following features: the unusual location of the *Enhydra* P4 lingual root, and the presence of

Table 4-4. Cranial and post-cranial characters in *Enhydritherium*, *Enhydriodon*, *Enhydra*, *Lutra*, and *Mustela*.

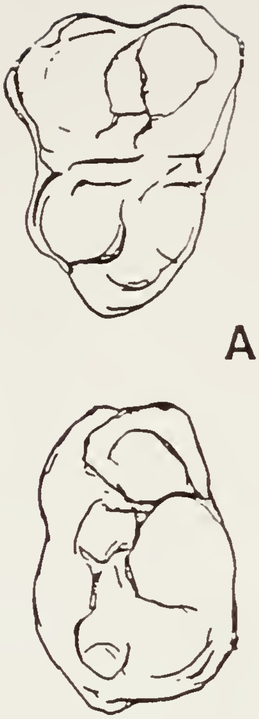
	Taxon				
Char.	E	Eh	Ea	L	M
CP*	broad	-	broad	narrow	narrow
NC	thick	-	thin	thin	thin
OF	deep	-	shallow	shallow	shallow
POP	absent	present	present	present	present
JF	prominent	-	small	small	small
MP	elongated	elongated	short	short	short
RA	shallow	shallow	steep	shallow	shallow
WF	broad	-	narrow	narrow	broad
SPP	P2=P3	-	P2<P3	P2<P3	P2<P3
LCP	absent	-	absent	present	absent
HC	present	present	?	absent	absent
PAS*	present	absent	absent	present	present
MMD*	> paraconid	<= paraconid	> paraconid	<= paraconid	<= paraconid
MTD*	squared off	rounded	squred off	rounded	rounded
OP*	reduced	-	reduced	not reduced	not reduced
UCP*	absent	-	absent	present	present
TM	reduced	-	not reduced	not reduced	not reduced
CT	slender	robust	robust	robust	robust
MTL**	short	short	long	long	long
GMP**	present	present	absent	absent	absent
HHP	present	-	absent	absent	absent
F	slender	-	robust	slender	slender

*: synapomorphy shared between *Enhydritherium* and *Enhydra*

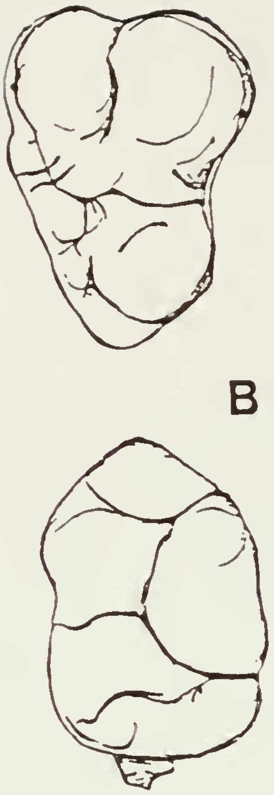
**: synapomorphy shared between *Enhydritherium* and *Enhydriodon*

abbreviations: E= *Enhydritherium*, Eh= *Enhydriodon*, Ea= *Enhydra*, L= *Lutra*, M= *Mustela*, CT= calcaneal tuber, CP= mandibular coronoid process, F= femur, GMP= grooved medial phalanx, HC= hypocone on P4 and M1; HHP= hypertrophied humeral processes, JF= jugal flange, LCP= lateral cingulum on p3, MMD= metaconid on m1, MTD= talonid on m1, MP= mastoid process, MTL= metatarsal length, NC= nuchal crest, OF= occipital fossa, OP= olecranon process, PAS= parastyle on P4, RA= rostral angle, SOP= supraorbital process, SPP= relative size of P2 to P3, TC= temporal crest, TM= tibial malleolus, UCP= ulnar coronoid process, WF= frontal width.

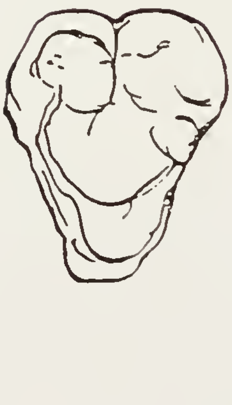
Figure 4-14. Illustrations of assorted otter carnassials (not to scale). A) permanent left P4 and m1 of Enhydritherium; B) permanent right P4 and left m1 of Enhydra (from Repenning, 1976); C) deciduous right P4 of Enhydritherium, showing anomalous cusp; D) permanent left P4 and right m1 of Lutra.



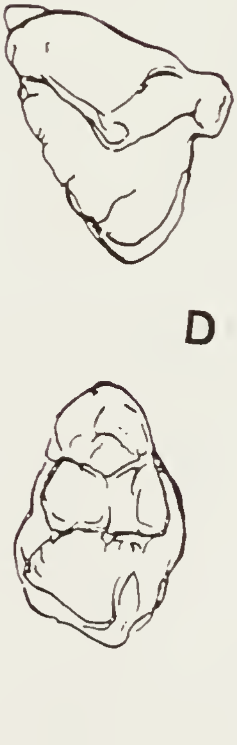
A



B



C



D

an anomalous cusp antero-medial to the "protocone" on an *Enhydra* dP4, interpretted by Repenning as the remnant of the true protocone (Figure 4-14). No similar remnant of a presumed protocone has been reported for an *Enhydra* M1. The plausibility of Repenning's proposal is unclear, and the status of the P4/M1 hypocone in *Enhydra* must be considered unresolved. It should be noted that the possible absence of a hypocone from *Enhydra* is not crucial to the issue of bunodont otter monophyly, since its presence in *Enhydritherium* and *Enhydriodon* would then be autapomorphic in this case. However, this situation would serve to disqualify both *Enhydritherium* and *Enhydriodon* as plausible ancestors of *Enhydra*, a hypothesis proposed by Repenning (1976).

No synapomorphies in Table 4-4 unite *Enhydra* with *Lutra*, and by the same token no synapomorphies unite *Enhydra* with both *Enhydritherium* and *Enhydriodon*, quite likely due in part to the large number of characters unknown for *Enhydriodon*. Potential bunodont otter synapomorphies (characters uniting *Enhydritherium* and *Enhydra* but unknown for *Enhydriodon*), excluding bunodonty, include a broad mandibular coronoid process, a reduced olecranon process, and the absence of an ulnar coronoid process. Of these characters, the broad mandibular process can be considered suspect due to a plausible functional correlation with bunodonty in mustelids, the same feature being present in the strong-jawed, facultatively durophagous *Meles* (Neal, 1977, 1986). Thus, two ulnar features independent of durophagy potentially unite the bunodont otters as a clade (verification of these characters as synapomorphies must await discovery of an *Enhydriodon* ulna).

Tentatively assuming that the bunodont otters are monophyletic, the question arises as to the phylogenetic relationships of *Enhydritherium*, *Enhydriodon*, and *Enhydra*. As noted above, two post-cranial synapomorphies unite *Enhydritherium* and *Enhydriodon* as sister taxa: short metatarsals and dorsally grooved medial phalanges. In contrast, Berta and Morgan (1985) cite the following dental synapomorphies uniting *Enhydritherium* and *Enhydra*: parastyle absent from the P4, m1 metaconid larger than the paraconid, and m1 talonid squared off (mandibular synapomorphies cited by Berta and Morgan have been shown to be erroneous; see above).

Thus, the post-cranial and dental lines of evidence directly conflict. There are two post-cranial synapomorphies versus three dental synapomorphies, and strict parsimony requires that the dental set of characters take precedence in evaluating these phylogenetic hypotheses. The total number of characters present in these sets is so small and the overall character state of *Enhydriodon* so poorly known however that strict parsimony is probably a poor guide in this instance. One could utilize a modified version of parsimony in evaluating these characters, weighing more heavily those characters that are least evolutionarily plastic and hence least prone to convergence. However, there is no clear basis for differentiating between these two sets of characters by this criterion as well. Therefore in conclusion, pending the discovery of additional evidence, the phylogenetic relationship between *Enhydritherium*, *Enhydriodon*, and *Enhydra* is best expressed as a trichotomy, with the fish-eating otters (represented by *Lutra*) designated a sister taxon (Figure 4-15).

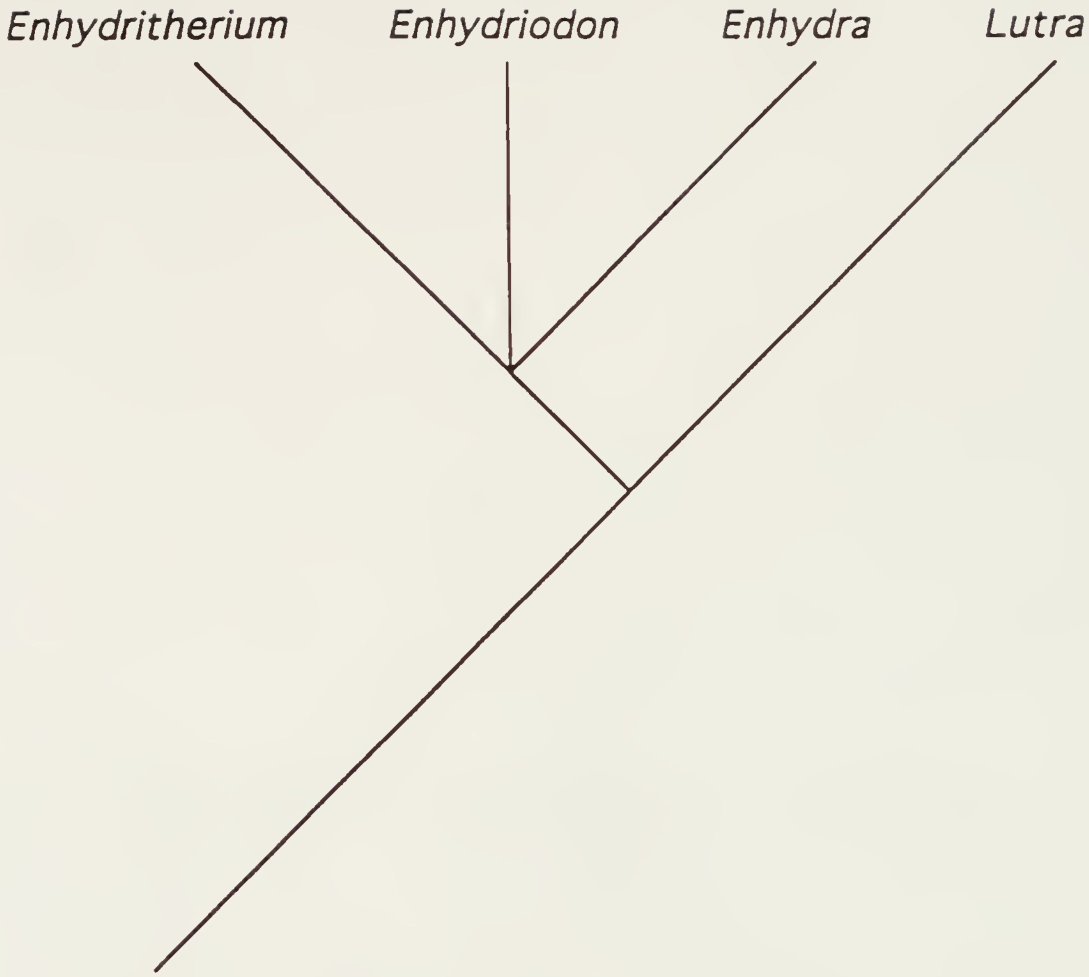


Figure 4-15. Cladocram showing a tentative hypothesis for the phylogenetic relationship between Enhydritherium, Enhydriodon, Enhydra, and Lutra.

CHAPTER 5

THE OSTEOLOGY OF THE GROUND SLOTH *PLIOMETANASTES* (XENARTHRA, MEGALONYCHIDAE)

The Great American Interchange between North and South America occurred in two distinct phases, one during the late Miocene(early Hemphillian/Huayquerian) and the other during the Pliocene (Blancan/Chapadmalalan). The second of these phases was the most important in terms of the number of exchanged taxa, a variety of ungulates, muroid rodents, and carnivores having dispersed southward while marsupials, caviomorph rodents and xenarthrans dispersed northward across the newly formed Panamanian Landbridge. This interchange had a strong impact on the faunas of both continents, though the most lasting effects were felt on South America (Webb, 1985; 1991). Less dramatic in a faunal sense but still noteworthy was the first phase of the Great American Interchange during the early Hemphillian (Huayquerian of South America). During this phase a single procyonid genus, *Cyonasua*, reached South America from North America while two ground sloth genera (*Pliometanastes*, family Megalonychidae; *Thinobadistes*, family Mylodontidae) reached North America from South America, the exchanges evidently involving sweepstakes dispersal across the Caribbean (Webb, 1985; Simpson, 1980). *Thinobadistes* was present in North America during both the early and late

Hemphillian, but failed to survive into the Pliocene latest Hemphillian. It left no descendent taxa in North America, post-Hemphillian North American mylodontid sloths such as *Glossotherium* having arrived separately during the second phase of the Great American Interchange (Webb, 1989). Unlike *Thinobadistes*, *Pliometanastes* survived into the latest Hemphillian and moreover underwent significant autochthonous evolution, giving rise to the well known genus *Megalonyx* during the latest Hemphillian. *Megalonyx* became widespread in North America during the Blancan and survived to the end of the Rancholabrean (Hirschfield and Webb, 1968; McDonald, 1977; and Kurten and Anderson, 1980).

The osteology of *Thinobadistes* is rather well known on the basis of an excellent sample of material from the early Hemphillian Mixon's Bone Bed in Florida, described by Webb (1989). In contrast, the osteology of *Pliometanastes* is relatively poorly known. The skull and dentition were described in detail by Hirschfield and Webb (1968), but the postcranial skeleton was left largely undescribed due to the of absence of material referrable to this genus. However a *Pliometanastes* specimen has been recovered from the late early Hemphillian Moss Acres Racetrack site in northern Florida by the Florida Museum of Natural History that fills a number of gaps in knowledge of *Pliometanastes* osteology. The specimem, UF 94500, is unusual in that it preserves an associated and largely complete right forelimb (including a virtually complete manus) and left hindlimb as well as an isolated string of caudal vertebrae, though cranial, dental, and other postcranial elements are absent. Nevertheless despite the overall incompleteness of the specimen, the local completeness of the limbs allows elements of _Pliometanastes_ to be described that were previously were unknown.

The purpose of this chapter is the description of this new Moss Acres Racetack _Pliometanastes_ material. Systematics are only briefly addressed, and no attempt is made to either resolve the exact phylogenetic relationship of this animal to other megalonychid sloths or formally erect new taxa. The morphological evolution of _Pliometanastes_ within North America is discussed however, as well as its implications for the correct species referral of the Moss Acres Racetrack specimen.

Materials and Methods

The Moss Acres Racetrack _Pliometanastes_ material was compared both with _Pliometanastes_ material from other sites (McGeehee and the Withlacoochee River 4A in Florida, both early Hemphillian to late early Hemphillian) and _Megalonyx_ material (both directly examined specimens and illustrations/verbal descriptions of specimens from three sources: Leidy, 1855; Stock, 1925, and McDonald, 1977). Illustrations and verbal descriptions of specimens were relied upon when actual specimens were unavailable for examination. All measurements were made with dial or tree calipers.

Systematics

Order Xenarthra

Suborder Pilosa

Family Megalonychidae

Pliometanastes Hirschfield and Webb, 1968

Pliometanastes protistus Hirschfield and Webb, 1968

?*Pliometanastes galushai* Hirschfield and Webb, 1968

The genus *Pliometanastes* contains only a single reliable species, *P. protistus*, *P. galushai* known only by a partial mandible. The referral of the Moss Acres Racetrack *Pliometanastes* to a species is problematic; the postcranial skeleton of Moss Acres Racetrack *Pliometanastes* resembles that of *P. protistus* from McGeehee in many respects, but also differs in a number of significant respects as well (see below). Unfortunately most of the diagnostic features of *P. protistus* are cranial (see Hirschfield and Webb, 1968). Thus the Moss Acres Racetrack (and perhaps the Withlacoochee River 4A) *Pliometanastes* may potentially represent a new species. Because of this uncertaintly, henceforth the Moss Acres Racetrack *Pliometanastes* will be referred to as simply *Pliometanastes* sp.

Description

Humerus

The Moss Acres Racetrack Pliometanastes includes single, largely intact right humerus (Figure 5-1). Measurements of this specimen are presented in Table 5-1. A number of Pliometanastes humeri are known from other sites. Hirschfield and Webb (1968) described three partial humeri from McGeehee, UF 9443. UF 9444, and UF 9445. Two undescribed partial humeri from McGeehee are also known, UF 23780 and UF 23781, as well as a nearly complete undescribed Pliometanastes humerus from Withlacoochee River 4A, UF 13794. Of these specimens, only the Moss Acres Racetrack and Withlacoochee River 4A humeri preserve the proximal ends.

The humeri from Moss Acres Racetrack, Withlacoochee River 4A, and McGeehee are all broadly similar. No significant differences were observed between the Withlacoochee River 4A and Moss Acres Racetrack humeri. However, humeri from these two sites differed from McGeehee humeri in their relative pectoral and deltoid crest development. The crests of the McGeehee humeri are much larger than those from the other two sites, while the ridge leading to the pectoral and deltoid crests on Moss Acres Racetrack/Withlacoochee River 4A is correspondingly poorly developed. The humerus of Pliometanastes strongly resembles that of Megalonyx as described by McDonald (1977). Similarities include the greater and lesser tubersities being equally developed, the head being nearly hemispherical, the

Figure 5-1. Left forelimb elements of *Pliometanastes* from Moss Acres Racetrack site (scale bar represents five centimeters). A) humerus, anterior view; B) humerus, close-up anterior view of the proximal end; C) radus, anterior view; D) ulna, anterior view.

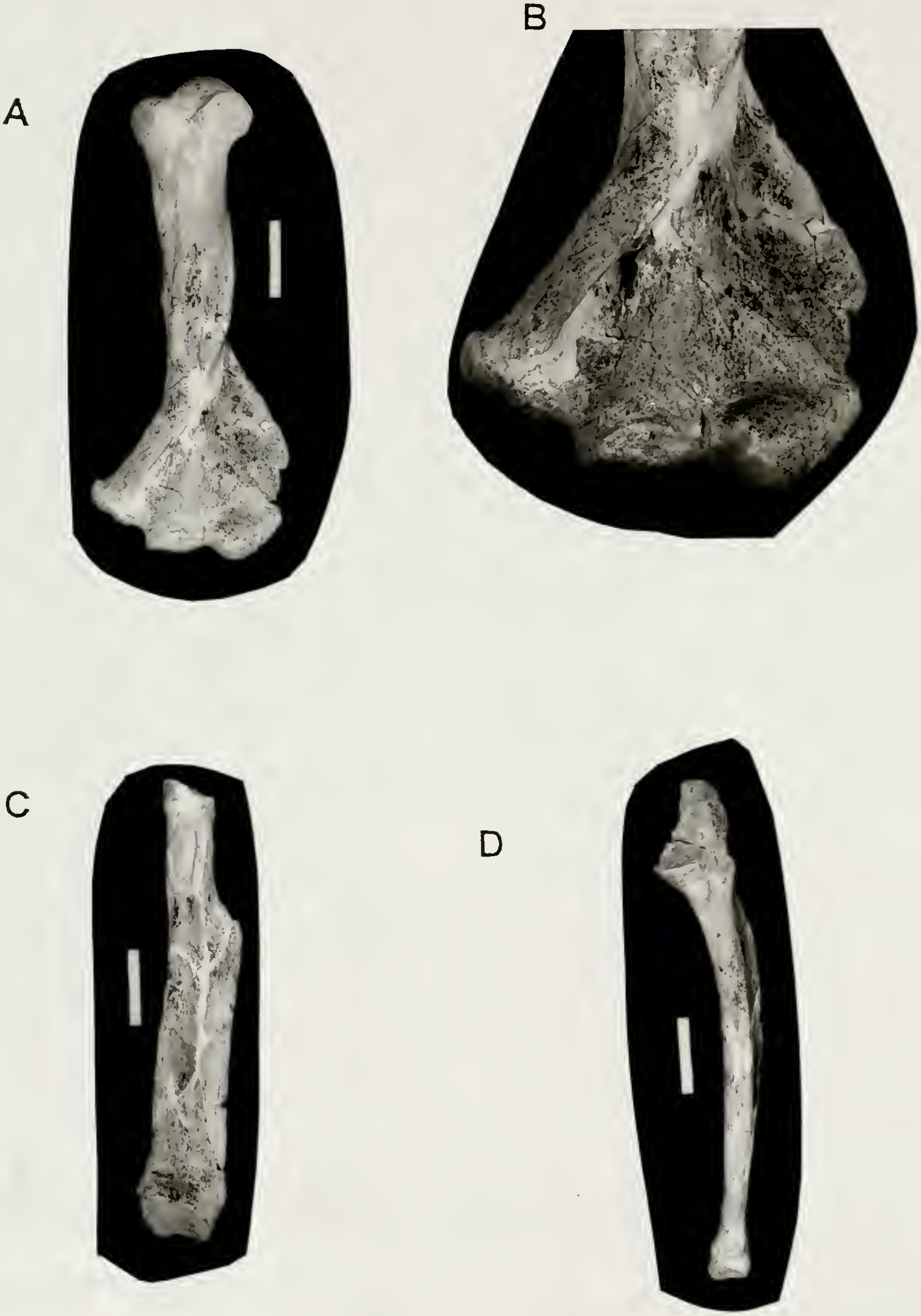

A
B
C
D

Table 5-1. Measurements (millimeters) of forelimb elements of UF 95400

Humerus	
total length:	390.0
width across distal edge (external-internal condyles):	127.4
width across tuberosities:	82.1
Radius	
total length:	291.5
width across distal edge:	52.3
width across proximal edge:	32.1
anteroposterior thickness at midpoint:	16.1
Ulna	
total length:from the olecranon process:	328.0
mediolateral thickness at midpoint:	22.6
maximum length of proximal articulating surface:	53.4
Scaphoid	
maximum length of the trapezoidal facet:	28.1
maximum length of the trapezium facet:	26.1
maximum length of the lunar facet:	29.9
maximum width of the posterior edge:	38.2
Lunar	
maximum length of the scaphoid facet:	28.1
maximum length of the cuneiform facet:	33.5
maximum mediolateral width:	23.1
Trapezium with fused metacarpal I	
total length:	38.0
width of the proximal end:	25.0
maximum width of the shaft:	26.9
maximum width of the distal end:	14.7
Unciform	
maximum mediolateral width:	27.8
maximum dorsoventral height:	26.0
Magnum	
length of the metatarsal III facet:	31.0
length of the unciform facet:	26.3
Cuneiform	
maximum mediolateral width:	37.2
maximum length of the unciform facet:	34.8
maximum length of the lunar facet:	29.6

Table 5-1--continued

Trapezoid	
maximum mediolateral width:	27.2
maximum dorsoventral height:	21.4
maximum anteroposterior length:	14.9
Metacarpal II	
total length:	56.7
maximum dorsoventral height, proximal end:	31.9
maximum dorsoventral height, distal end:	31.3
maximum mediolateral width, proximal end:	25.8
maximum mediolateral width, distal end:	21.2
minimum dorsoventral height of the shaft:	15.7
minimum mediolateral width of the shaft:	19.3
Metacarpal III	
total length:	61.3
maximum dorsoventral height, proximal end:	30.2
maximum dorsoventral height, distal end:	35.5
maximum mediolateral width, proximal end:	32.1
maximum mediolateral width, distal end:	26.1
minimum dorsoventral height of the shaft:	18.4
minimum mediolateral width of the shaft:	23.2
Metacarpal IV	
total length:	69.2
maximum dorsoventral height, proximal end:	25.6
maximum dorsoventral height, distal end:	34.0
maximum mediolateral width, proximal end:	18.0
maximum mediolateral width, distal end:	20.0
minimum dorsoventral height of the shaft:	16.2
minimum mediolateral width of the shaft:	13.9
Metacarpal V	
total length:	62.0
maximum dorsoventral height, proximal end:	19.1
maximum dorsoventral height, distal end:	20.4
maximum mediolateral width, proximal end:	19.3
maximum mediolateral width, distal end:	13.5
minimum dorsoventral height of the shaft:	9.0
minimum mediolateral height of the shaft:	14.1
Medial phalanx, digit I	
total length:	24.1
dorsoventral height, proximal end:	18.3
dorsoventral height, distal end:	12.8
mediolateral width, proximal end:	11.5
mediolateral width, distal end:	12.0

Table 5-1--continued

Proximal phalanx, digit II	
total length:	21.4
maximum dorsoventral height:	non measurable
maximum mediolateral width:	21.5
Medial phalanx, digit II	
total length:	40.0
dorsoventral height, proximal end:	26.1
dorsolventral height, distal end:	19.9
mediolateral width, proximal end:	19.8
mediolateral width, distal end:	16.5
Ungual phalanx, digit II	
total length:	85.0
dorsoventral height, proximal end:	33.0
mediolateral height, proximal end:	21.0
Medial phalanx, digit III	
total length:	43.3
dorsoventral height, proximal end:	30.1
dorsoventral height, distal end:	24.9
mediolateral width, proximal end:	24.4
mediolateral width, distal end:	18.0
Ungual phalanx, digit III	
total length:	104.4
dorsoventral height, proximal end:	44.1
mediolateral width, proximal end:	23.3
Proximal phalanx, digit IV	
total length:	22.0
dorsoventral height, proximal end:	29.6
dorsoventral height, distal end:	23.2
mediolateral width, proximal end:	19.7
mediolateral width, distal end:	18.0
Medial phalanx, digit IV	
total length:	48.5
maximum dorsoventral height:	26.9
maximum mediolateral width:	19.7
Ungual phalanx, digit IV	
total length:	85.0
dorsoventral height, proximal end:	36.8
mediolateral width, proximal end:	22.8

Table 5-1--continued

Medial phalanx, digit V	
total length:	24.2
dorsoventral height, proximal end:	18.2
dorsoventral height, distal end:	10.7
mediolateral width, proximal end:	13.2
mediolateral width, distal end:	12.1
Ungual phalanx, digit V	
total length:	43.1
dorsoventral height, proximal end:	26.2
mediolateral width, proximal end:	16.2

outline of the distal articulation surface resembling a figure-eight, and the biccipital groove being nearly absent. The strong resemblance of the *Pliometanastes* humerus to that of *Megalonyx* is consistent with findings by Hirschfield and Webb (1968) that the humeri of megalonychid sloths are generally strongly conservative.

Radius

The Moss Acres Racetrack *Pliometanastes* preserves a single right radius, the first such element ever discovered for *Pliometanastes* (Figure 5-1). Measurements are presented in Table 5-1. Comparisons with *Megalonyx* are based on McDonald (1977). The head is roughly circular as in *Megalonyx*, though it is slightly broader mediolaterally than anteroposteriorly. The ulnar facet is distinctly oblate and nearly directly superior to the biccipital tuberosity, contrasting *Megalonyx* in which the ulnar facet is semicircular and restricted to the posterior surface of the head. The biccipital tuberosity is positioned almost completely on the anterior surface and extends mediolaterally, contrasting *Megalonyx* in which it extends medially. Like *Megalonyx* the shaft shows only a slight medial curvature, is equidimensional over the proximal one-fourth in cross-section, and is highly flattened mediolaterally over the distal three-fourths of the shaft. On the lateral surface the mediolateral flattening begins just below the biccipital tuberosity, abruptly broadening the shaft greatly. The mediodistal edge of the shaft is roughened for articulation with the ulna, and a suprastyloid process is present as in Megalonyx. The distal articulation is deeply concave and bounded by three processes, one lateral (the styloid), one posteromedial, and one anteromedial. Ridges connect the anteromedial process to both the connected styloid and posteromedial processes, contrasting Megalonyx in which an additional ridge connects the posteromedial and styloid processes as well.

Ulna

A single, well preserved ulna is present (Figure 5-1). Measurements are presented in Table 5-1. Previously the ulna of Pliometanastes was known on the basis of a single poorly preserved distal end, UF 9447 from McGeehee, described by HIrschfield and Webb (1968). Comparison of the Moss Acres Racetrack ulna with UF 9447 reveals the follwing differences. The radial notch of the Moss Acres Racetrack specimen is much smaller than that of McGeehee, is positioned more laterally, is nearly confluent with the trochlear notch rather than being separated by a ridge as in McGeehee, and is widest anteroposteriorly rather than proximodistally as in McGeehee. The olecranon process of the Moss Acres Racetrack specimen is short and anteroposteriorly broad relative to that of McGeehee. In addition, the Moss Acres Racetrack olecranon is smoothly tapered with its broadest section immediately above the trochlear notch, contrasting McGeehee in which the olecranon is distinctly indented just above the trochlear notch, with the posterior edge of this indentation a thin ridge. A fossa for the flexor digitorum profundus is present on the medial surface of the proximal end of the ulna in both specimens, though this fossa is both shallower and shorter in the Moss Acres Racetrack specimen than in that from McGeehee. The process for the insertion of the brachialis, immediately distal to the coronoid process on the anterior edge, is much larger in Moss Acres Racetrack than in McGeehee.

Additional comparison of the Moss Acres Racetrack ulna is made with *Megalonyx*, based on illustrations in Stock (1925). The size and position of the trochlear notch are almost identical in both the Moss Acres Racetrack *Pliometanastes* and *Megalonyx*. As in *Megalonyx* the coronoid is large and extends medially to form a shelf over the fossa for the flexor digitalis profundus. The radial notch is the same relative size and in the same position in both Moss Acres Racetrack and *Megalonyx*,, though it is irregularly shaped in *Megalonyx* and distinctly rounded in Moss Acres Racetrack. Like *Megalonyx*, the mediolaterral curvature of Moss Acres Racetrack is small, with the distal three-fourths of the shaft virtually straight. Also as in *Megalonyx* there is a well developed crest on the lateral edge of the anterior surface, ranging from the middle to the distal one-fourth section of the shaft.

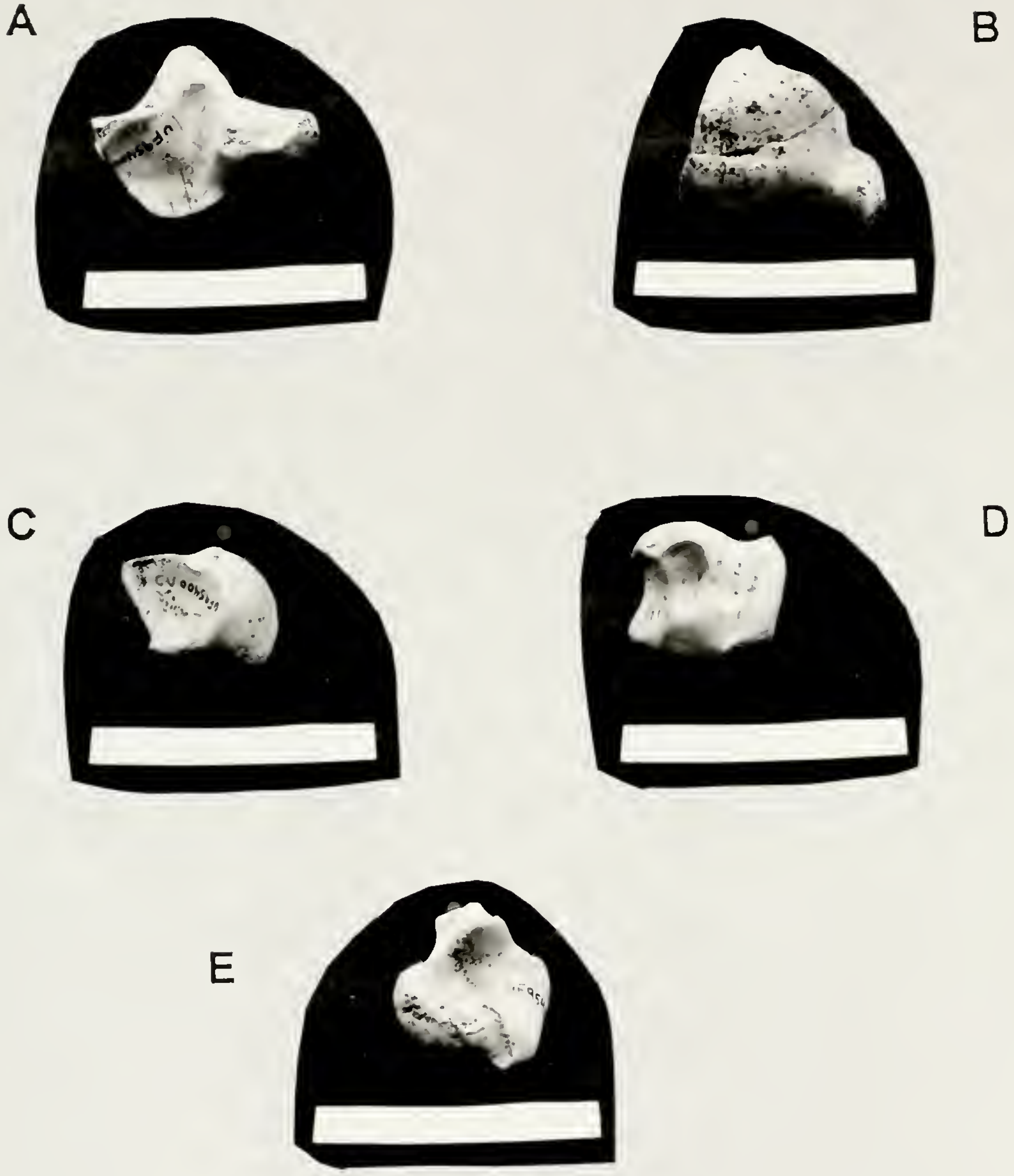
Scaphoid

The scaphoid in Moss Acres Racetrack is represented by two specimens, a well preserved left specimen associated with the specimen UF 94500 (Figure 5-2), and a single isolated right specimen, UF 69947. UF 69947 is the only *Pliometanastes* specimen known from Moss Acres Racetrack that is separate from UF 94500, and it is identical to the scaphoid of UF 94500 in both its size and morphology Measurements of both specimens are presented in Table 5-1. The scaphoid of *Pliometanastes* is undescribed in the literature, but a specimen from Withlacoochee River 4A, UF 23591, is referred to *Pliometanastes* and is used for comparison. The Moss Acres Racetrack and Withlacoochee River 4A scaphoids are essentially indistinguishable. The radial articulating surface in both is crudely rectangular in profile, though postero-laterally there is a thick projection that follows the lunar facet and postero-medially a projection follows the trapezium facet. The lunar facet is broad and crescentic. Below the lunar facet lies a pit-like, rounded fossa bordered posteriorly by the magnum facet. The trapezoid facet is roughly triangular, though somewhat constricted ventrally so as to appear crooked. The trapezium facet is elongated and vaguely tongue-shaped, though quite broad at the base.

Lunar

The lunar, previously unknown for *Pliometanastes*, is represented by a single left specimen (Figure 5-2).

Figure 5-2. Left carpal elements of *Pliometanastes* from Moss Acres Racetrack site (scale bar represents five centimeters). A) scaphoid, distal view; B) scaphoid, proximal view; C) lunar, lateral view; D) unciform, distal view; E) unciform, proximal view.


A
B
C
D
E

Measurements are presented in Table 5-1. A comparison is made with the Megalonyx lunar UF 23542. As in Megalonyx the radial articulating surface is strongly arched. However the arch is greater in Megalonyx, and a deep pit in the proximal portion of the groove present in Megalonyx is absent from that of Pliometanastes. The scaphoid facet, on the medial surface, is roughly semicircular dorsally, while ventrally it has two fossae separated by a trapezoid-shaped magnum facet that is confluent with the scaphoid facet (in Megalonyx these fossae form one continuous fossa). The Pliometanastes magnum facet projects below the body of the lunar to form a distinct prong, contrasting Megalonyx in which the magnum articulation is a fossa contained within the body of the lunar. The lateral surface tapers distally with the medial surface to form a ventral wedge, and is dominated by a shallow, tear-drop shaped fossa for articulation with the cuneiform that is square-shaped in Megalonyx. Like Megalonyx the dorsal surface is triangular in shape, with one vertex pointed laterally, and the palmar surface is coarse in texture and irregularly shaped with a shallow concavity.

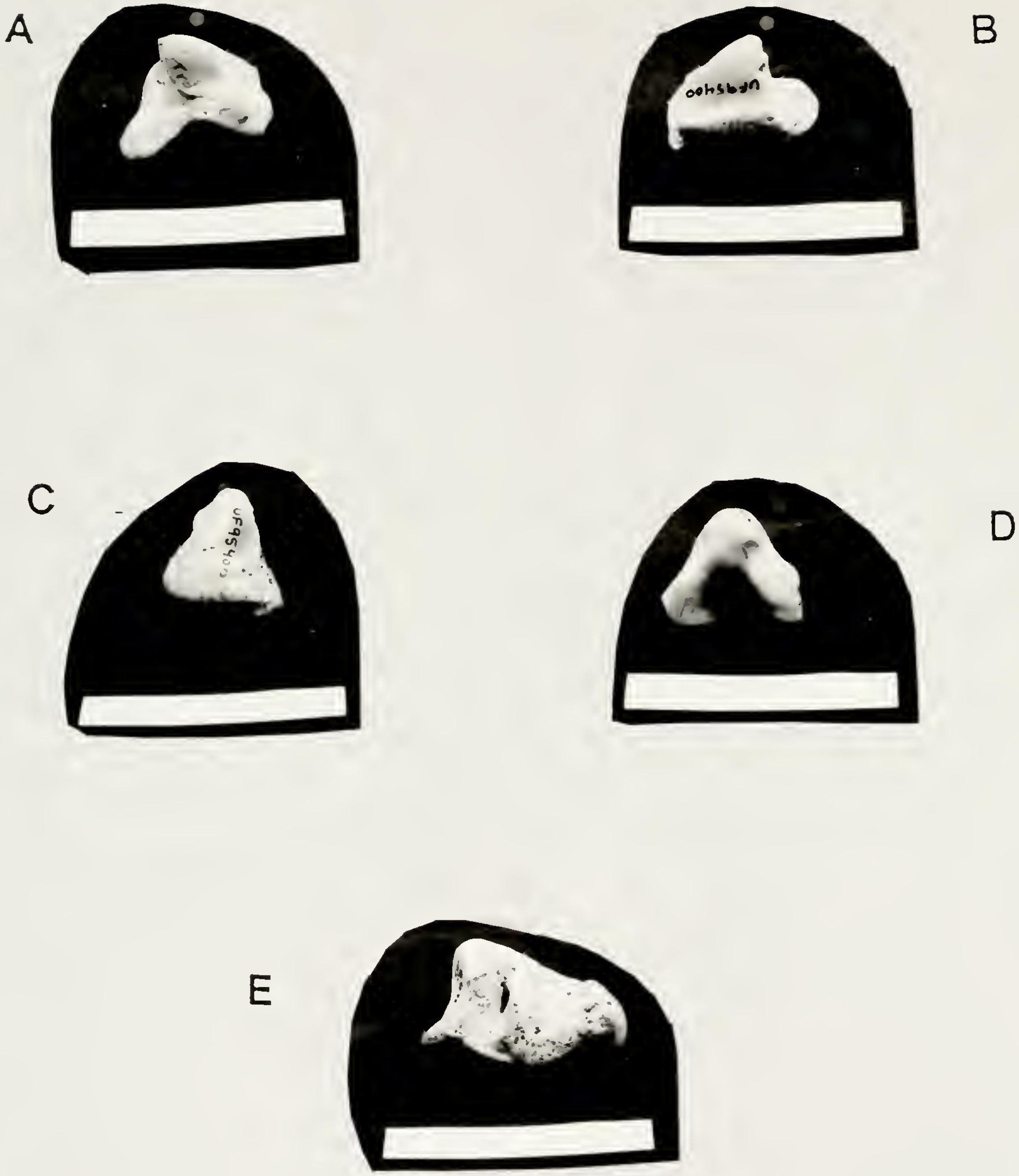
Unciform

The unciform is represented by a single left specimen, and like the scaphoid is previously unknown for Pliometanastes (Fig. 5-2) Measurements are presented in Table 5-1. It is compared with the Megalonyx specimen UF 23544. The Moss Acres Racetrack Pliometanastes unciform strongly resembles that of Megalonyx, and differs significantly only in the following respects: 1) a large convex facet immediately over the metacarpal III articulating surface is present in the Pliometanastes unciform but absent from Megalonyx; and 2) the facet for the magnum is trapezoidal in the Pliometanastes specimen rather than crescent-shaped as in Megalonyx.

Magnum

The magnum is represented by a single left specimen, and like other carpals of Pliometanastes discussed above is previously undescribed (Figure 5-3). Measurements are presented in Table 5-1. No actual specimens or illustrations of the magnum of Pliometanastes or Megalonyx were available for comparison. The medial surface of the Moss Acres Racetrack magnum is characterized by a prominent projection that forms a major part of the articulation with metacarpal III. The articulation with the metacarpal III is composed of two parts, a large upper crescent-shaped fossa and two lower facets that partially merge to form a "figure-eight" pattern. The posterior surface contains the unciform facet, which is roughly rectangular with the long axis dorso-ventral. The ventral surface is crescent-shaped and smooth, while the dorsal surface is irregularly shaped with a coarse texture.

Figure 5-3. Left carpal elements of *Pliometanastes* from Moss Acres Racetrack site (scale bars represent five centimeters). A) magnum, medial view; B) magnum, lateral view; C) trapezoid, proximal view; D) trapezoid, distal view; E) fused trapezium and metacarpal I, lateral view.


A
B
C
D
E

Trapezoid

The trapezoid of Moss Acres Racetrack is represented by a single left specimen, and is previously undescribed for *Pliometanastes*.(Figure 5-3) Measurements are presented in Table 5-1. A comparison is made with the *Megalonyx* trapezoid UF 23916. Like that of *Megalonyx* the trapezoid of the Moss Acres Racetrack specimen is triangular in proximo-distal profile, with the broadest side (equals the base) on its ventral surface and the vertex on the dorsal surface, the vertex narrower in *Megalonyx* than *Pliometanastes*. Proximally the trapezoid is uniformly concave, the concavity deeper in Moss Acres Racetrack than *Megalonyx*, for articulation with the scaphoid. Distally there is both a concave lateral surface and a convex medial surface for articulation with metacarpal II. Lastly, a facet of unknown function is present on the palmar surface, considerably larger in *Megalonyx* than in the Moss Acres Racetrack specimen.

Cuneiform (=Pyramidiform)

The cuneiform of the Moss Acres Racetrick *Pliometanastes* is well preserved. It is essentially indistinguishable from that of *Megalonyx*.

Trapezium and Fused Metacarpal I

As in *Megalonyx* (McDonald, 1977) the trapezium of *Pliometanastes* is fused with metacarpal I to form a single structure. A single left trapezium/metacarpal I is included in the Moss Acres Racetrack specimen, the only one of its kind ever found for Pliometanastes.(Figure 5-3). Measurements are presented in Table 5-1. The Moss Acres Racetrack Pliometanastes specimen is compared with the Megalonyx specimens UF 23910A and B. The point of fusion between the trapezium proper and metacarpal I is indicated by a strong mediolateral constriction; in Pliometanastes this constriction is associated with a corresponding "dimple" at approximately one-third the proximal length of the structure that is absent from Megalonyx. The trapezium portion of the Pliometanastes element roughly resembles that of Megalonyx;. However the base of the Pliometanastes specimen is considerably broader than that of Megalonyx, while the facet for articulation with metacarpal II is distinctly flattened in Moss Acres Racetrack and set on a stalk in Megalonyx. The metacarpal portion of these elements, in contrast, differs considerably between these two taxa. In the Moss Acres Racetrack specimen the neck of the structure is indistinct, being little narrower than the head, while the head itself is a smooth, rather featureless ball. In Megalonyx in contrast the neck is obvious, being considerably narrower than the head, and the head retains rudimentary typical metacarpal features such as a carina and lateral ridges.

Metacarpal II

Most of the metacarpals of Pliometanastes are described by Hirschfield and Webb (1968). Measurements of the Moss

Acres Racetrack right metacarpal II are presented in Table 5-1. Comparison of the Moss Acres Racetrack left metacarpal II with the described specimen UF 11524 from Withlacoochee River 4A, referred to _P. protistus_, reveals no significant differences between the two.

Metacarpal III

As in the case of metacarpal II, the left metacarpal III of Moss Acres Racetrack does not differ significantly from the _Pliometanastes protistus_ specimen UF 11525 from McGeehee described by Hirschfield and Webb (1968). Measurements are presented in Table 5-1.

Metacarpal IV

Measurements are presented in Table 5-1. As in metacarpals II and III, the left metacarpal IV of Moss Acres racetrack strongly resembles the _Pliometanastes protistus_ specimen UF 16637 from McGeehee described by Hirschfield and Webb (1968). However two significant differences exist: 1) a groove on the palmar surface of the proximal end of the metacarpal is much larger in the McGeehee specimen than that from Moss Acres Racetrack; and 2) the proximal articulating surface is broad in proximodistal profile in the Moss Acres Racetrack specimen, while in the one from McGeehee it is constricted medially so as to resemble a "figure-eight."

Metacarpal V

Measurements of the Moss Acres Racetrack specimen are presented in Table 5-1. The metacarpal V of Pliometanastes protistus has been described by Hirschfield and Webb (1968) on the basis of the specimen UF 23583 from McGeehee. Comparison of the McGeehee specimen with the single left Moss Acres Racetrack Pliometanastes metacarpal V reveals a number of significant differences. On the latero-proximal surface of the Moss Acres Racetrack specimen the facet for metacarpal IV is narrower and longer than that from McGeehee, and bordered by ventral and dorsal ridges absent from McGeehee. Dorso-proximally the unciform facet of the Moss Acres Racetrack specimen is considerably smaller than that of McGeehee, while distally the Moss Acres Racetrack head is distinctly less robust than that from McGeehee.

Phalanges of the Manus

Digits I-V of the Moss Acres Racetrack Pliometanastes manus are represented by phalanges, though the series is not complete for each digit. The phalanges represented for each digit are as follows: I- medial, II- proximal, medial, and distal, III- medial and distal, IV- proximal, medial, and distal, and V- medial and distal. Measurements are presented in Table 5-1. This sample is considerably larger than the Pliometanastes sample described by Hirschfield and Webb (1968), who list a single proximal phalanx of digit III and and five distal phalanges, one probably belonging to digit

III (none of these phalanges was specified as belonging to either the manus or pes).

The Moss Acres Racetrack phalanges II-V are compared with some of those known for Pliometanastes from McGeehee and described by Hirschfield and Webb (1968), specificallly UF 9459 (proximal) and UF 18953 (distal, probably digit V). The proximal phalanx is virtually indistinguishable in these two populations. The ungual phalanges were also very similar. Comparison of the Moss Acres Racetrack and McGeehee ungual phalanx V shows only a single difference, the Moss Acres Racetrack specimen having a well developed process on the ventral surface of the ungual sheath absent from McGeehee. The medial Moss Acres Racetrack phalanx, otherwise unknown for Pliometanastes, is compared to the medial phalanx of Megalonyx based on illustrations in Leidy (1855). The proximal articulation facets of the Pliometanastes medial phalanx are shallower than those of Megalonyx, while the lateral facet walls extend farther forward so that unlike Megalonyx the central carina is exposed and visible in side view. In addition, the shaft of the Moss Acres Racetrack specimen is more heavily tapered and dorsoventrally flattened with a longer neck than that of Megalonyx.

Other interesting features are visible in the phalanges of the Moss Acres Racetrack manus. First, the proximal phalanx of digit V is unusual compared to all of the other Moss Acres Racetrack proximal phalanges in lacking a groove in its proximal articulating surface, possessing instead a simple smooth fossa. More interesting still is the medial phalanx of digit I. Phalanges are completely absent from digit I of _Megalonyx_ (McDonald, 1977). However, the Moss Acres Racetrack _Pliometanastes_ evidently possessed both a proximal and a medial phalanx, though the presence of a distal phalanx is doubtful (see below). The digit I medial phalanx of the Moss Acres Racetrack _Pliometanastes_ has the following features. The proximal articulating surface is broad, concave, and vaguely saddle-shaped, resembling medial phalanx V in lacking a carina..The shaft has a short though distinct neck, with dorsal and ventral grooves extending onto the head (presumably passages for tendons). The head is well developed but lacks a clear articulation surface; the distal end is distinctly rugose and lacks a carina, indicating the absence of a proximal phalanx for digit I.

Femur

A well preserved left femur has been recovered from Moss Acres Racetrack, the first ever found for _Pliometanastes_ (Figure 5-4). The measurements for this specimen are presented in Table 5-2. Due to the lack of other _Pliometanastes_ specimens, comparison of the Moss Acres Racetrack femur is made with the femur of _Megalonyx_ based on illustrations in Leidy (1855).

The femoral balls of _Pliometanastes_ and _Megalonyx_ are quite similar, though Moss Acres Racetrack has a somewhat larger articulation surface. The necks and the greater

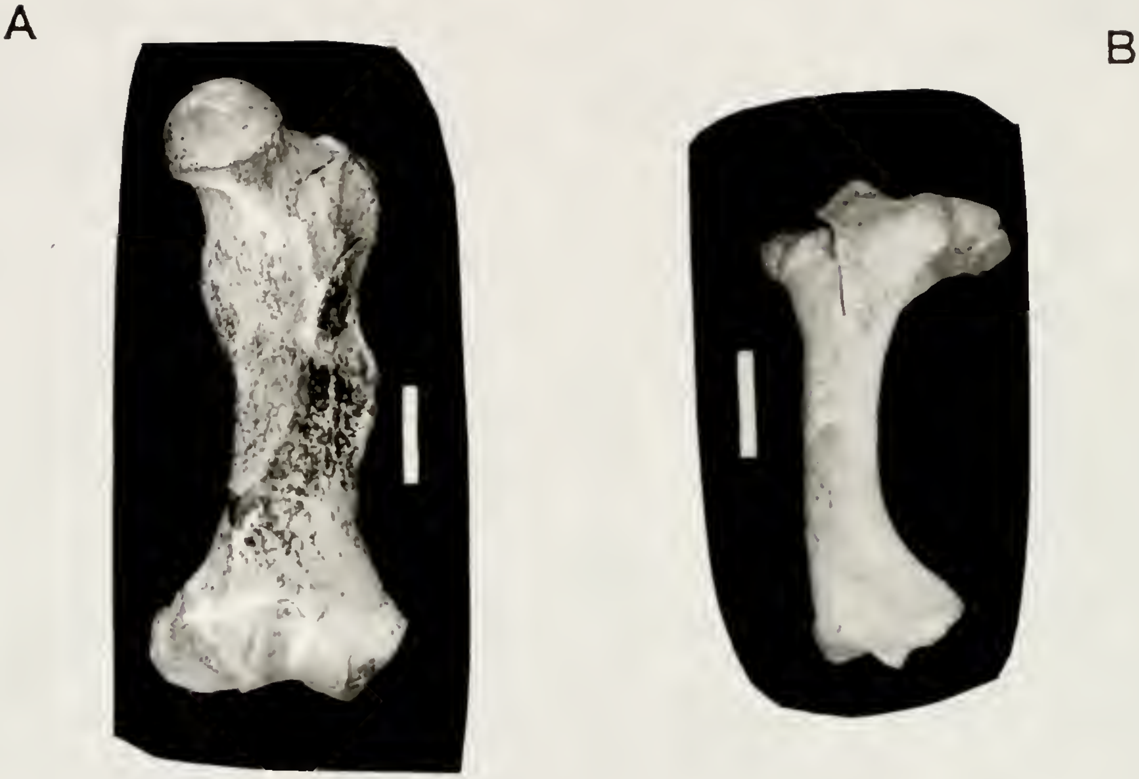


Figure 5-4. Left hindlimb elements of *Pliometanastes* from Moss Acres Racetrack (scale bar represents five centimeters). A) femur, anterior view; B) tibia, anterior view.

Table 5-2. Measurements (millimeters) of hindlimb elements of UF 95400

Femur	
total length from the ball to the medial condyle:	303.5
distance from the ball to the greater trochanter:	125.5
ball diameter:	63.2
maximum distance between the epicondyles:	55.1
maximum distance between the condyles:	113.5
maximum mediolateral width at the lesser trochanter:	76.0
maximum anteroposterior thickness at the lesser trochanter:	42.3
Tibia	
total length:	221.4
maximum anteroposterior width, proximal end:	101.5
maximum anteroposterior width, distal end:	45.0
maximum mediolateral width, proximal end:	104.2
maximum mediolateral width, distal end:	84.2
minimum anteroposterior shaft width:	27.0
minimum mediolateral shaft width:	43.3
Calcaneum	
maximum width of the posterior astragalar facet:	36.6
maximum width of the medial astragalar facet:	32.8
thickness of the tuber base anterior to the posterior astragalar facet:	29.7
Astragalus	
mediolateral width at the anterior edge:	51.4
mediolateral width at the midpoint::	44.2
mediolateral width at the posterior edge:	25.4
maximum width at the navicular facet:	30.2
length of the posterior calcaneal facet:	42.1
maximum length of the medial calcaneal facet:	29.3
midline anteroposterior length:	58.3
Navicular	
maximum mediolateral width:	44.0
maximum dorsoventral height:	42.8
maximum anteroposterior thickness:	19.4
Metatarsal I	
total length:	33.0
maximum dorsoventral height:, prrximal:	27.9
maximum dorsoventral height, distal:	21.1
maximum mediolateral width, proximal:	18.0
maximum mediolateral width, distal:	15.9
minimum dorsoventral height of the shaft:	14.8
minimum mediolateral width of the shaft:	16.5

Table 5-2--continued

Metatarsal II	
not measurable	
Metatarsal III	
total length:	47.1
dorsoventral height, proximal:	31.9
dorsoventral height, distal:	44.5
mediolateral width, proximal:	27.0
mediolateral width, distal:	33.3
minimum dorsoventral shaft height:	27.2
minimum mediolateral shaft width:	30.8
Metatarsal IV	
total length:	69.0
dorsoventral height, proximal:	32.1
dorsoventral height, distal:	35.8
mediolateral width, proximal:	26.2
mediolateral width, distal:	21.7
minimum dorsoventral shaft height:	19.0
minimum mediolateral shaft width:	16.6
Metatarsal V	
dorsoventral height of proximal end:	60.0
maximum mediolateral width across metatarsal IV facet:	26.0
maximum dorsoventral height across metatarsal IV facet:	22.2
maximum mediolateral width of tuber:	23.1
minimum mediolateral width at proximal edge:	10.4
Medial phalanx, digit I	
total length:	25.4
dorsoventral height, proximal:	21.7
dorsoventral height, distal:	12.1
mediolateral height, proximal:	15.3
mediolateral height, distal:	13.5
Ungual phalanx, digit I	
minimum total length (specimen broken at tip):	47.5
dorsoventral height, proximal:	22.2
mediolateral height, proximal:	17.0
Proximal phalanx, digit II	
total length:	24.3
maximum dorsoventral height:	33.2
maximum mediolateral width:	23.1

trochanters are also similar, though the fossa within the greater trochanter is somewhat longer and broader in Pliometanastes than in Megalonyx. The lesser trochanter is relatively somewhat shorter in Pliometanastes than Megalonyx, with the lateral third trochanter similar in both. The shafts of the two animals are significantly different. The shaft of Megalonyx is broader than that of Pliometanastes and its width is uniform along most of its length, contrasting Pliometanastes whose shaft is distinctly tapered proximo-distally and disto-proximally to form an hour glass-like constricted neck roughly at the middle. Proximally, the medial epicondyle is enlarged relative to the lateral epicondyle to form an offset patellar groove in Pliometanastes, while in Megalonyx the two epicondyles are of equal size. In addition the epicondyles on the whole are considerably more robust in Pliometanastes. The condyles are similar in these two animals, except that in Pliometanastes the lateral condyle is expanded proximally to encompass a process that is distinctly separate in Megalonyx.

Tibia

As with the femur, the tibia of Pliometanastes is previously unknown, so comparisons with the Moss Acres Racetrack left tibia are made using Megalonyx illustrations in Leidy (1855) (see Figure 5-4). Measurements are presented in Table 5-2. Overall the tibiae of Pliometanastes and Megalonyx are quite similar, though they differ in some relatively minor features. In Megalonyx the articulation surface with the femur is relatively level. However in Pliometanastes this surface is distinctly angled with the lateral surface higher, resulting in a medial deflection of the femoro-tibial joint absent from Megalonyx (this medial deflection may explain the enlargement of the medial femoral condyle of the Moss Acres Racetrack individual, which in this limb position would have supported a greater load than the lateral condyle). Both Pliometanastes and Megalonyx have a facet for the cyamelle (a sesamoid) on the postero-cranial region of the lateral femoral articulation surface, though in Pliometanastes the facet is separated from the rest of the femoral articulation by a much shallower groove than that of Megalonyx. In addition both Pliometanastes and Megalonyx have highly developed anterior, tibial, and interosseous crests.

Patella

A presumably left patella is preserved from Moss Acres Racetrack, but its condition is so poor that comparative examination is impossible. The patella of Pliometanastes is otherwise unknown.

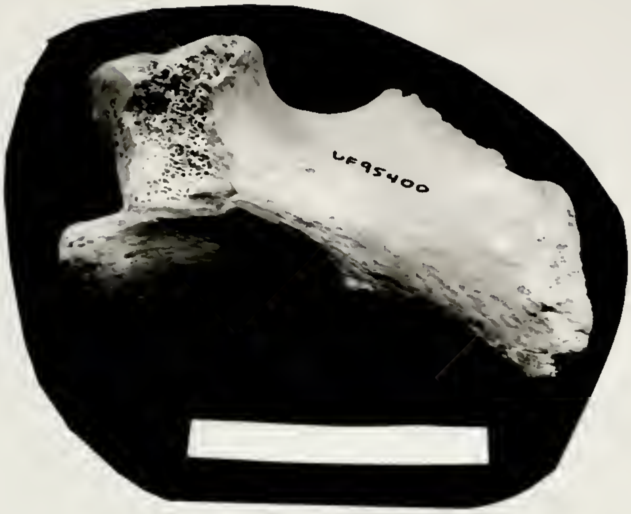
Calcaneum

The tuber of the Moss Acres Racetrack left calcaneum is absent, though the rest of the bone is reasonably well preserved (Figure 5-5). Measurements are presented in Table

5-2. The calcaneum of Pliometanastes protistus is described by Hirschfield and Webb (1968), and comparisons here are made with the McGeehee specimen UF 9442. The cuboidal facet of the Moss Acres Racetrack Pliometanastes specimen is damaged, so a shape comparison with the McGeehee specimen cannot be made for this feature. However the positions of the facets are similar in the two specimens, though the pillar of bone containing the cuboid facet is taller in the McGeehee specimen than than that of Moss Acres Racetrack. Moreover this pillar contains a groove lateral to the posterior astragalar facet that is broader, deeper, and straighter in the McGeehee specimen than that of Moss Acres Racetrack. The medial astragalar facets are similar, though the Moss Acres Racetrack facet is somewhat broader posteriorly and more elongated than that of McGeehee. However, the posterior astragalar facets differ considerably; in the McGeehee specimen it extends laterally beyond the cuboidal facet to form a lateral shelf, whereas in Moss Acres Racetrack the facet abuts solidly against the base of the cuboidal facet. Both the Moss Acres Racetrack and McGeehee specimens have a lateral tuberosity separated from the posterior astragalar facet by a groove. However, the groove is broader and the tuberosity more mediolaterally elongated in the McGeehee specimen than that of Moss Acres Racetrack.

Figure 5-5. Tarsal elements of *Pliometanastes* from Moss Acres Racetrack site (scale bars represent five centimeters). A) partial calcaneum, ventral view; B) partial calcaneum, showing astragalar articulation surface; C) metatarsal I, lateral view; D) metatarsal I, proximal articulation surface.

A



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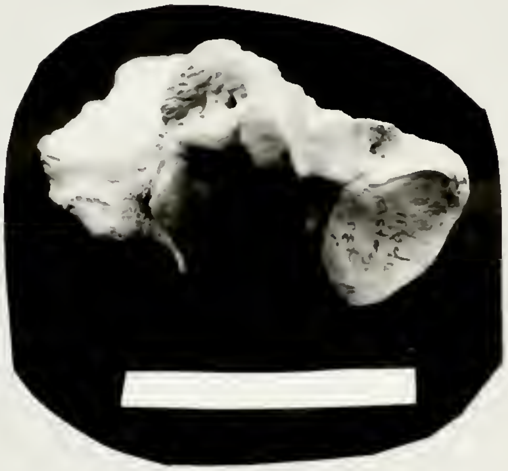

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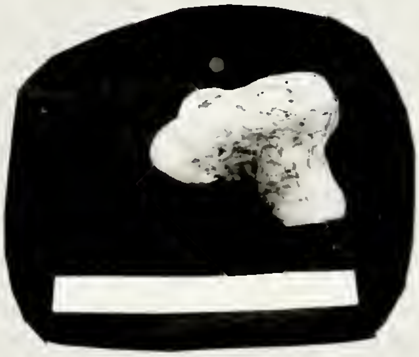

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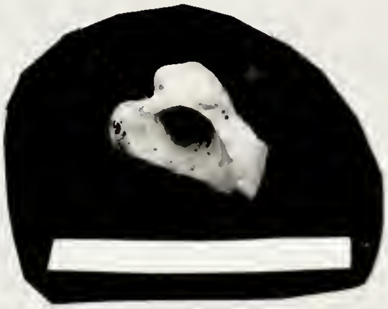


Astragalus

A single left astragalus is represented from Moss Acres Racetrack. Measurements are presented in Table 5-2. The astragalus of *Pliometanastes protistus* was described in detail by Hirschfield and Webb (1968) based on McGeehee material. Comparison of the McGeehee specimen UF 9441 with the Moss Acres Racetrack specimen reveals the two to be virtually indistingushable, with the only significant difference being a navicular facet that is medio-ventrally narrower and dorso-ventrally taller in Moss Acres Racetrack than McGeehee.

Navicular

The single left navicular represented from Moss Acres Racetrack closely resembles that of the *Pliometanastes protistus* from McGeehee described by Hirschfield and Webb (1968). Comparison of the Moss Acres Racetrack specimen with the McGeehee specimen UF 9474 reveals them to be be essentially indistinguishible.

Metatarsal I

The metatarsal I, represented by a single left specimen in Moss Acres Racetrack, was previously unknown for *Pliometanastes* (Figure 5-5). Measurements are presented in Table 5-2. No specimens or illustrations of a *Pliometanastes* or *Megalonyx* metatarsal I were available for comparison. The *Pliometanastes* metatarsal I is highly foreshortened, having a well developed head but virtually no neck. The proximal articulation surface is dominated by a large, rounded fossa. with a dorso-medial thick projection including part of the posterior portion of the articulation surface. Dorso-medially, the proximal end has a thick projection, including the posterior part of the articulation fossa, with a flat, rounded facet on top presumably for articulation with metatarsal II. More mediallly, a large, distinctly rounded process extends from the proximal articulation fossa to the middle of the shaft neck, separated from the dorsomedial process by a distinct groove. Ventrally a third process exists, extending forward to form a ridge on the lateral surface of the shaft. Distally the carina is large, with only the lateral ridge present.

Metatarsal II

Metatarsal II is present, but is represented only by part of the distal carina and two partial but apparently well developed ridges.

Metatarsal III

Metatarsal III is previously unknown for *Pliometanastes*, so the left specimen from Moss Acres Racetrack is compared with an illustration of *Megalonyx* from Stock (1925). Measurements are presented in Table 5-2 The proximal surface for articulation with the ectocuneiform overall is similar between *Megalonyx* and *Pliometanastes*, though that of

Megalonyx is distinctly constricted in the middle. The only other significant differences between the *Pliometanastes* metatarsal III and that of *Megalonyx* are that the *Pliometanastes* shaft is relatively shorter than that of *Megalonyx*, and that the *Pliometanastes* metatarsal articulation is concave rather than flat.

Metatarsal IV

Measurements of the Moss Acres Racetrack metatarsal IV are presented in Table 5-2. The metatarsal IV of *Pliometasnastes protistus* is described by Hirschfield and Webb (1968) based on the McGeehee specimen UF 23580. Comparison of the two specimens reveals no significant differences.

Metatarsal V

The Moss Acres Racetrack metatarsal V is incomplete, lacking the lateral blade-like process for insertion of the peroneus brevis muscle. Thus, the description encompasses only the distal articulation and the proximal tarsal articulation. Measurements are presented in Table 5-2. Metatarsal V is known from McGeehee by the specimen UF 19278, but is undescribed by Hirschfield and Webb. The shaft of the Moss Acres Racetrack specimen is broader than that from McGeehee, and the flattened shaft merges with the lateral blade rather than being separated by a distinct neck as in the McGeehee specimen. The heads of the two specimens are similar, though the Moss Acres Racetrack neck is considerably shorter than that of McGeehee. The facets for metatarsal IV are similar in these two specimens, but cuboid facet is broader in Moss Acres Racetrack than in McGeehee.

The metatarsal V's of both Moss Acres Racetrack and McGeehee as *Pliometanastes* representatives are compared to the metatarsal V of *Megalonyx* based on illustrations and descriptions from Stock (1925) and McDonald (1977). Both *Pliometanastes* and *Megalonyx* have a broad lateral process for insertion of the peroneus brevis, and both also are similar in the location and shape of cuboid and metatarsal IV facets. However, *Megalonyx* resembles the Moss Acres Racetrack *Pliometanastes* over the McGeehee *Pliometanastes* in having a shaft that is broad and relatively short without a clear neck, though it more closely resembles the McGeehee *Pliometanastes* in having a medial shaft edge that is straight rather than curved as in the Moss Acres Racetrack *Pliometanastes*.

Phalanges

Digits I-V of the pes are represented by phalanges, though only II-IV have complete sets. Measurements are presented in Table 5-2. The phalanges of digits I-IV are all virtually identical beyond size, and in turn are indistinguishable from the phalanges of the manus (thus, the possibility that pedal phalanges were identified as manual phalanges and vice versa cannot be discounted). Digit V, represented by only a proximal phalanx, alone appears to be derived. As in the proximal phalanx of the manus digit V, the proximal metapodial articulation is concave and lacks a distinct groove, not surprising considering the absence of a keel from metatarsal V. The distal end is rather irregular in form with a pair of deep dorsal and ventral grooves, the ventral groove giving way to a thick tuberosity (presumably the grooves and the tuberosity represent tendon attachment sites).

The Evolution of *Pliometanastes* in North America

The *Pliometanastes* specimens examined in this study came from three sites: Moss Acres Racetrack, Withlacoochee River 4A, and McGeehee Farm. Though these sites are all Hemphillian in age, McGeehee Farm is considered to be earliest Hemphillian (approximately 9 million years old) while Moss Acres Racetrack and Withlacoochee River 4A are considered to be late early Hemphillian (approximately 7 million years old) (Tedford et al., 1987; Hulbert, 1988). Thus, there is a geologically significant chronological separation between the McGeehee Farm site and Moss Acres Racetrack/Withlacoochee River 4A sites, and thus a corresponding potential for significant autochthonous evolutionary change in *Pliometanastes*.

Circumstantial evidence for such autochthonous evolution can be found by doing a careful comparison of the *Pliometanastes* specimens from McGeehee, Withlacoochee River 4A, and Moss Acres Racetrack. Had autochthonous evolution occurred in Pliometanastes over the course of the early Hemphillian, one would expect that individuals from Moss Acres Racetrack and Withlacoochee River 4A would be essentially indistinguishable from each other, and that both would show common significant differences from McGeehee individuals. Examination of the limited sample of specimens discussed in the preceding section reveals the following. In the three cases where Moss Acres Racetrack and Withlacoochee River 4A elements could be directly compared (the humerus, metacarpal II, and the scaphoid) the elements were found to be essentially indistinguishable, a finding consistent with (though not proving outright, due to the incredibly small sample size) the hypothesis that the Withlacoochee River 4A and Moss Acres Racetrack animals are conspecifics. However, comparison of Moss Acres Racetrack (and in one case Withlacoochee River 4A) Pliometanastes elements with those from McGeehee reveal that out of ten elements compared, six show clear differences, four of them (the humerus, the ulna, the calcaneum, and metatarsal V) significant. Such differences in clearly related, chronologically separated animals strongly suggests that Pliometanastes experienced significant evolution during this time period, though whether this evolution was cladogenetic or anagenetic is unclear (see below).

The strong possibility that the Moss Acres Racetrack/Withlacoochee River 4A Pliometanastes evolved from the older McGeehee Pliometanastes leads to the question of the taxonomic status of these animals. Do both animals belong to the species *Pliometanastes protistus*, or should the Moss Acres Racetrack/Withlacoochee River 4A *Pliometanastes* be referred to a new species? The answer to this question depends on how one interprets the morphological differences between the McGeehee and the Moss Acres Racetrack/Withlacoochee River 4A animals. Most of the morphological differences between these two animals appear to be adaptively neutral (e.g., differences in the shape of articulation surfaces in the carpals, tarsals, and metapodials). Thus, based on the evidence currently available, there is no reason to believe that the McGeehee *Pliometanastes* occupied an adaptive niche significantly different from that of the Moss Acres Racetrack/Withlacoochee River 4A *Pliometanastes*. This inference leads to two possible conclusions. (1) The McGeehee and Moss Acres Racetrack/Withlacoochee River 4A *Pliometanastes* represent two distinct species separated by a cladogenetic event, with major morpho-ecological differences between them either nonexistent, extremely subtle, or else revealed by elements yet to be observed in one of the animals in question (e.g., the cranium of the Moss Acres Racetrack/Withlacoochee River 4A *Pliometanastes*). (2) The Moss Acres Racetrack/Withlacoochee River 4A *Pliometanastes* is the result of gradual anagenetic evolution from the McGeehee *Pliometanastes*, with the differences between them being as much the result of evolutionary drift as strict channeling by natural selection. If conclusion 1 above is correct, then there is no question but that the Moss Acres Racetrack (and in all likelihood the Withlacoochee River 4A) _Pliometanastes_ should referred to a new species. If conclusion 2 is correct, however, then the taxonomic status of the two animals is ambiguous; in this case, the Moss Acres Racetrack/Withlacoochee River 4A _Pliometanastes_ could at best be considered a chronospecies, with little to be gained by formally referring it to a new species (see Wiley, [1981] for a discussion of the problems associated with formally erected evolutionary species). At the moment, the available evidence is insufficient for determining whether conclusion 1 or 2 is the more plausible. Thus, pending the discovery of additional evidence, the most prudent course is to simply refer the Moss Acres Racetrack/Withlacoochee River 4A _Pliometanastes_ to _Pliometanastes_ sp. or _P_. cf. _protistus_.

CHAPTER 6

THE OSTEOLOGY OF PEDIOMERYX HEMPHILLENSIS (ARTIODACTYLA, DROMOMERYCIDAE) AND THE PALEOECOLOGICAL SIGNIFICANCE OF SIZE TRENDS IN THE PEDIOMERYX LINEAGE

The dromomerycids are an extinct group of strictly North American horned pecoran ruminants that are known over most of the Miocene and the earliest Pliocene, ranging from the Arikareean to the latest Hemphillian (Webb, 1983a). The dromomerycids are a difficult group to diagnose, and at least partly because of this there has been considerable controversy concerning their phylogenetic relationship to the other pecorans. The dentitions of the dromomerycids are reminiscent of those of cervids, especially in their heavily molarized p4's.. As a consequence they have often been included within the Cervidae (e.g. Frick, 1937; Stirton, 1936; Dahlquest, 1983; and Schultz, 1977), though they lack deciduous horns, i.e. antlers (see below). Romer (1966, p: 285)) included the dromomerycids with the paleomerycids, which were defined by him as a group of conservative higher pecorans that "show many of the features to be expected in the ancestors of the deer and giraffes but are difficult to assign to either family and appear to represent a common ancestral stock." Janis (1986) proposed that the dromomerycids are the sister group to both the cervid and hoplitomerycid ruminants. One group of dromomerycids, relegated to the subfamily Cranioceratinae by Webb (1983a), is unique relative to all other pecorans in possessing a single occipital horn as well as paired frontal horns. The earliest known cranioceratine dromomerycid is *Barbouromeryx*, an Arikareean to Hemingfordian genus that is characterized by a mere occipital swelling rather than a true horn, as well as small frontal horns. *Bouromeryx*, ranging from the Hemingfordian to the Barstovian, resembles *Barbouromeryx* in the development of its occipital horn but is more advanced in having larger frontal horns. The first cranioceratine with a distinct occipital horn rather than a mere swelling was *Cranioceras*, which ranged from the Barstovian to the Clarendonian. The last cranioceratine and indeed dromomerycid was *Pediomeryx*, which appeared in the late Clarendonian and survived to the latest Hemphillian (Webb, 1983a).

Webb (1983a) divided *Pediomeryx* into two subgenera, *Pediomeryx* (*Yumaceras*) and *Pediomeryx* (*Pediomeryx*), on the basis of differences in molar crown height, diastema length, and overall body size (see discussion below). Of these two subgenera, *P*. (*Yumaceras*) is the best known, the species *P*. (*Y*.) *hamiltoni* having been described by Webb (1983a) on the basis of a rich sample of material including horn cores from the late Clarendonian Love Bone Bed of Florida. In contrast *P*. (*Pediomeryx*), containing the single species *P*. (*P*.) *hemphillensis*, is known on the basis of relatively limited material with its horn cores unknown. *Pediomeryx* material referred to *P*. (*P*.) *hemphillensis* has been collected from the Moss Acres Racetrack site, including a partial skull with all three horn cores, two mandibles, a maxilla, and an assortment of postcranial elements. This sample of *Pediomeryx hemphillensis* is significant because it represents possibly the largest single sample of this species ever found from a single locality, and because it preserves the first horn cores ever found for this subgenus and species.

Materials and Methods

The *Pediomeryx* material from the Moss Acres Racetrack site wias extensively compared with horn cores and dental material of *P*. *hamiltoni* from the Love Bone Bed in the collection of the Florida Museum of Natural History in Gainesville, Florida. The Moss Acres Racetrack braincase was compared with a personally owned *Odocoileus* skull, no adequate dromomerycid skulls or skull illustrations being available. Illustrations of *Pediomeryx hemphillensis* specimens from Stirton (1936), Dahlquest (1983), and Frick (1937) were used for comparative purposes in examining Moss Acres Racetrack dentition. Measurements of unobserved *Pediomeryx* specimens were taken from Webb (1983a). All measurements of observed specimens were made with dial calipers.

Systematics

Order Artiodactyla

Family Dromomerycidae

Subfamily Cranioceratinae Webb, 1983a

Pediomeryx Stirton, 1936

Pediomeryx (*Pediomeryx*) Stirton, 1936

Pediomeryx (*Pediomeryx*) *hemphillensis* Stirton, 1936

The systematics of *Pediomeryx* and *P*. *hemphillensis* in particular have been a point of controversy and confusion, due in part to a dispute over the validity of the genera *Yumaceras* and *Procoileus*. Stirton (1936) established the dromomerycid genus and species *Pediomeryx hemphillensis* on the basis of dentition, while Frick (1937) established the genus and species *Yumaceras figginsi* on the basis of a horn core; he also established another species of *Yumaceras*, *Y*. *falkenbachi*, on the basis of dentition. *Yumaceras falkenbachi* was synonymized with *Pediomeryx hemphillensis* by Stirton (1944), leaving *Yumaceras figginsi* as a monotypic species. However Webb (1983a), after examining the large sample of *Pediomeryx* material including both dentition and horn cores from the Love Bone Bed, showed that *Yumaceras* was a synonym of *Pediomeryx*, though the species *P*. *figginsi* was valid. The genus *Procoileus* with the single species *P*. *edensis* was established by Frick (1937) on the basis of an isolated partial mandible. However both Stirton (1944) and Webb (1983a) showed that *Procoileus edensis* is indistinguishible from *P*. *hemphillensis*.

Description

Skull

The Moss Acres Racetrack Pediomeryx partial skull UF 69945 is the only skull known for the species P. hemphillensis, and perhaps the entire genus Pediomeryx. The cranium proper of this specimen is largely intact, with both the two frontal horn cores and the occipital horn core present (Figure 6-1). However the facial portion of the skull is largely absent, with only the right orbit and postorbital bar preserved. A small part of the face is also preserved in the isolated maxilla associated with this specimen described below, namely the nasal and lacrimal region, but this bone is too heavily crushed to reveal any significant detail. The occipital region is well preserved, with the proximal portion of the occipital horn core, foramen magnum, nuchal crest, nuchal prominence, and occipital condyles all intact. The most striking aspect of the occiput is the broad, rhomboidal expansion of the posterior surface of the occipital horn core, presumably for insertion by an exceptionally large splenius muscle. The braincase is moderately preserved, the cranial roof and posterior floor (formed by the occipital, basioccipital, and part of the basisphenoid) being largely intact (a partial endocranial cast is also present). Overall the surviving braincase closely resembles that of the cervid Odocoileus, though it differs in having a much narrower valley at the junction

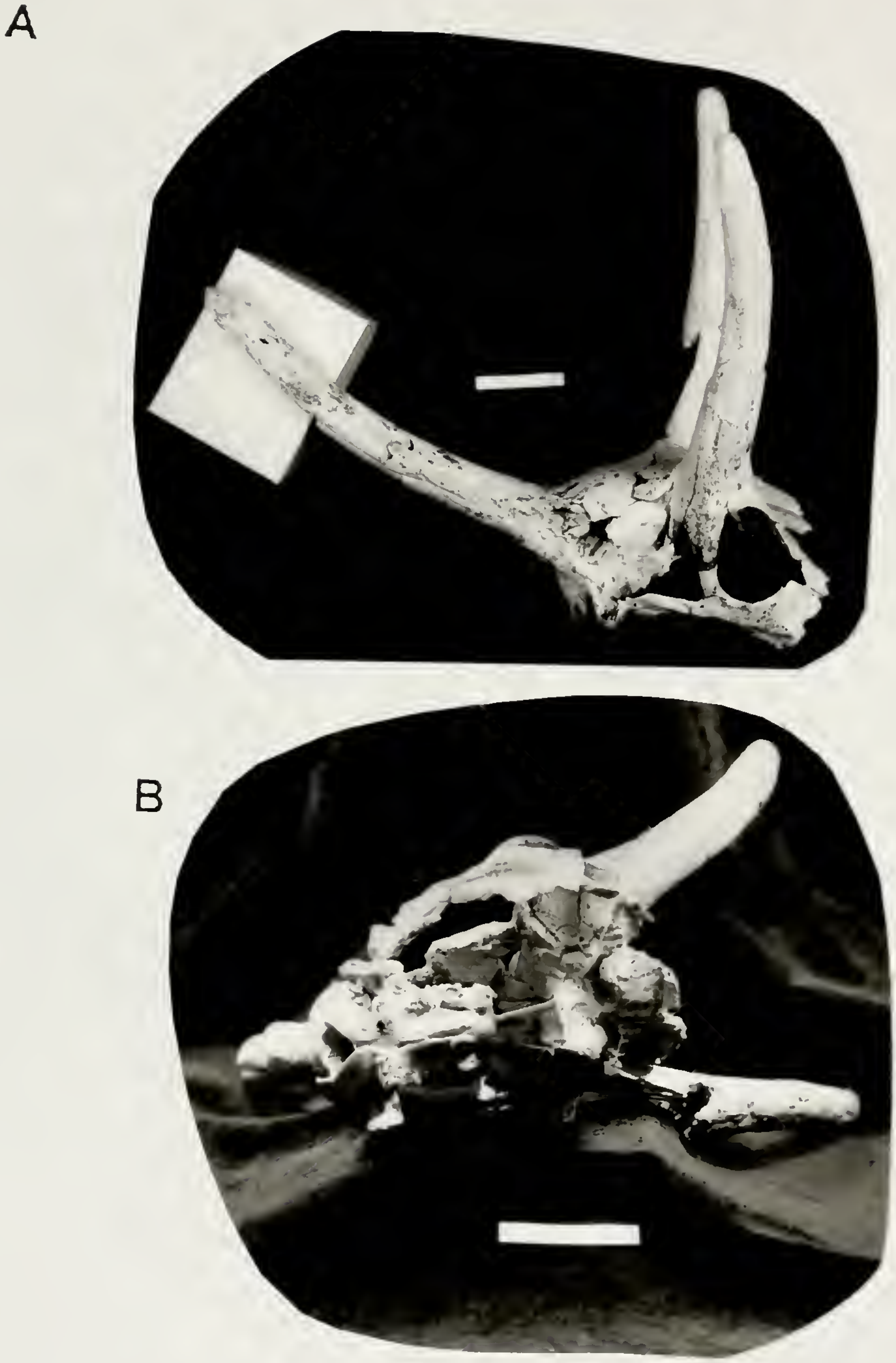


Figure 6-1. The partial skull of *Pediomeryx* (scale bars represent five centimeters). A) lateral view; B) ventral view.

between the basisphenoid and basioccipital. The paraoccipital processes are also intact, and differ from those of *Odocoileus* in being relatively broad and untapered. Neither the auditory bullae nor any basicranial foramina are preserved.

On the whole the three horn cores of the skull are all well preserved, though the left frontal has taken considerable damage proximally. Measurements of the horn cores are presented in Table 6-1. Morphologically the Moss Acres Racetrack horn cores resemble those of *P. hamiltoni*, though those of *P. hamiltoni* are considerably larger. Frick (1937) portrayed the horn cores of dromomerycids with palmate, antler-like distal tips attatched to burrs where dehiscence was presumed to have taken place, a portrayal based on Frick's belief that the dromomerycids were true cervids rather than any direct evidence. Webb (1983a) showed that burrs and other signs of deciduousness are absent from the horn cores of *P.hamiltoni* and that their distal tips are relatively simple, ruling out cervid-like shedding and suggesting a similarity to such non-shedding pecorans as the bovids, giraffids, and antilocaprids. As in *P. hamiltoni*, palmate tips and burrs are absent from the Moss Acres Racetrack horn cores.

Despite the overall similarity however, there are significant morphological differences between the horn cores of *P. hamiltoni* and *P. hemphillensis*. Looking at the measurements presented in Table 6-1, it is apparent that the

Table 6-1. Comparative measurements (millimeters) for *Pediomeryx hemphillensis* horn cores, cranium UF 69945 (both frontal and occipital), and *P. hamiltoni* frontal (UF 27104) and occipital (UF 27103).

specimen	bapw	bmlw	mapw	mmlw	dapw	dmlw	tl
UF 69945 frontal	31.6	29.0	25.2	25.0	19.6	19.5	194.5
UF 27104	49.3	34.0	30.9	29.4	19.8	21.0	229.0
UF 69945 occipital	31.6	29.0	25.2	25.o	19.6	19.5	215.0
UF 27103	40.4	26.3	31.7	23.2	14.9	24.1	243.0

abbreviations: bapw= basal anteroposterior width, bmlw= basal mediolateral width, mapw= middle anteroposterior width, mmlw= middle mediolateral width, dapw= distal tip anteroposterior width, dmlw= distal tip mediolateral width, tl= total length.

occipital horn core of *P. hamiltoni* is far more mediolatally flattened at the base and middle sections than that of the Moss Acres Racetrack specimen. In addition a pair of deep lateral grooves that extend from the base to the tip are present on the lateral surface of the *P. hamiltoni* occipital horn core, grooves that are absent from the Moss Acres Racetrack occipital horn core. The frontal horn cores of these two species are more similar than their occipital horn cores. Nevertheless, as in the occipital horn cores the base of the *P. hamiltoni* frontals are much more mediolaterally flattened than those of the Moss Acres Racetrack specimen, though this flattening vanishes distally. A lateral groove is present on the frontal horn cores of both animals; however the groove on the Moss Acres Racetrack specimen is relatively shallow and extends from the base to at most the middle to the horn core (the actual extent is indeterminant due to damage to the distal portion of the specimen), while that of *P. hamiltoni* is much deeper and extends from the base to the very tip of the horn core, wandering onto the latero-posterior surface near the tip.

Mandible

Two *Pediomeryx* mandibles have been recovered from Moss Acres Racetrack, one nearly completely intact (UF 69945) associated with the skull described above and the other preserving only the middle portion of the ramus (UF 97267) (Figure 6-2). Measurements of these mandibles as well as

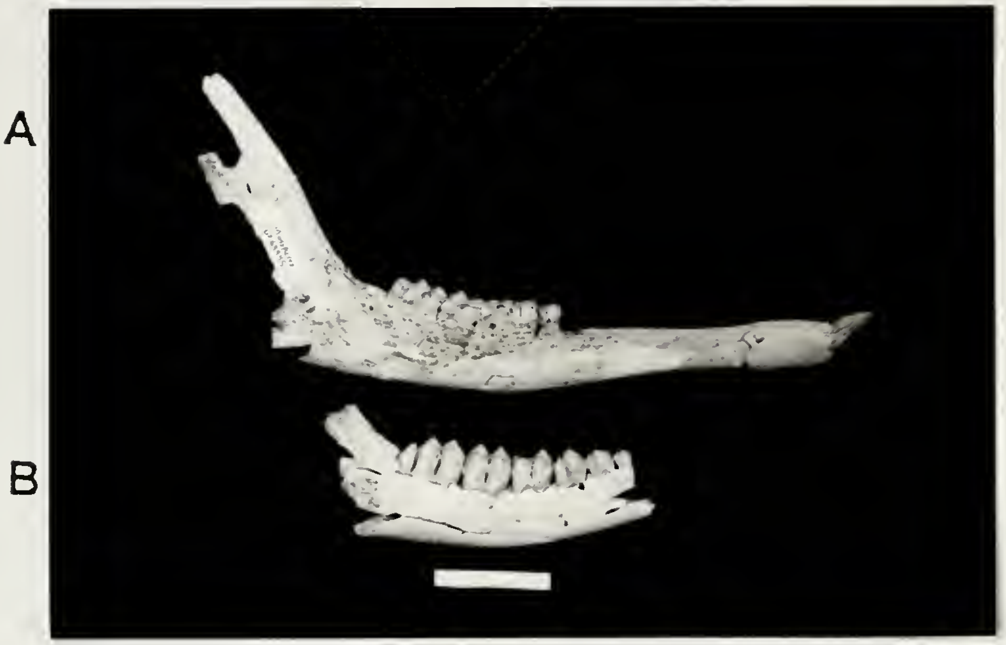


Figure 6-2. Mandibles of *Pediomeryx hemphillensis* from Moss Acres Racetrack site (scale bar represents five centimeters). A) UF 69945; B) UF 97267.

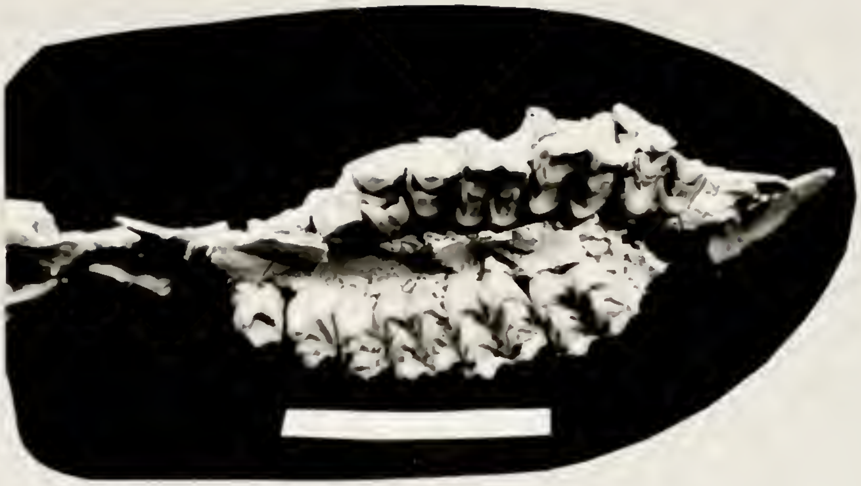
those of other of other *Pediomeryx* mandibles are presented in Table 6-2. It is clear from the measurements in Table 6-2 that the mandibles of *Pediomeryx hemphillensis* are similar in total length to those of *P. hamiltoni*. However, they are strikingly different in their relative robustness, the mandibular ramus of *P. hamiltoni* being much deeper than that of *P. hemphillensis*. This greater mandibular robustness in *P. hamiltoni* contradicts the claim made by Webb (1983a) that the molars of *P. hemphillensis* are more hypsodont than those of *P. hamiltoni*.

Dentition

The upper dentition of *Pediomeryx* is represented from Moss Acres Racetrack only by the single maxilla of the skull UF 69945, which preserves the entire toothrow from P2-M3 (Figure 6-3). Measurements of these teeth are presented in Table 6-3. No significant samples of *P. hemphillensis* upper dentition are described in the literature, and thus qualitative and quantitative comparisons with other *P. hemphillensis* specimens are impossible. Morphological comparison of these teeth with those of *P. hamiltoni* from the Love Bone Bed reveal the following differences: P3 with a distinct protocone and hypocone, contrasting the P3 of *P. hamiltoni* which lacks lingual cusps; molars with tightly closed fossettes, contrasting the molars of *P. hamiltoni* which are relatively open; M2 and M3 entostyles well developed, contrasting *P. hamiltoni* whose M2 and M3

Figure 6-3. Dentition of *Pediomeryx hemphillensis* from Moss Acres Racetrack (scale bars represent five centimeters). A) upper dentition, UF 69945; B) lower dentition, UF 69945; C) lower dentition, UF 97267.

A



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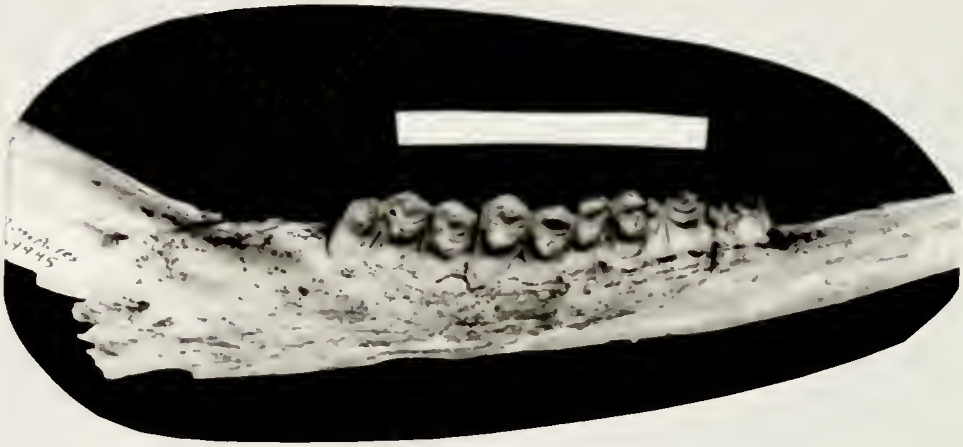

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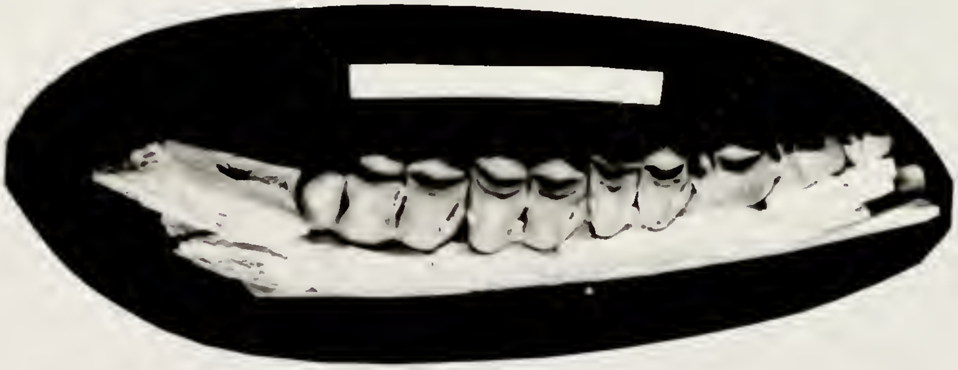

Table 6-2. Comparative measurements (millimeters) of *Pediomeryx hemphillensis* mandibles UF 69945 and UF 97267, and *P. hamiltoni* mandibles UF 27217 and UF 27004.

specimen	lcmf	ld	lp2m3	drfm3	trfm3
UF 69945	255.0	109.0		31.7	16.6
UF 97267			97.9	30.0	16.7
UF 27217	251.0			40.0	21.7
*UF 27004		86.4			

* value taken from Webb (1983)

abbreviations: lcmf= length from the coronoid process tip to the mental foramen, ld= length of the diastema, drfm3= depth of the ramus internally at the front of the M3, trfm3= thickness of the ramus internally at the front of the M3.

Table 6-3. Comparative measurements (millimeters) of *Pediomeryx hemphillensis* upper dentition (maxilla UF 69945) with *Pediomeryx hamiltoni* (average values from Webb [1983]).

	P. hemphillensis		*P. hamiltoni*	
tooth	length	width	length	width
P2	9.2	9.3	15.1	13.6
P3	9.7	13.0	14.6	17.8
P4	9.4	14.2	14.0	17.5
M1	13.1	16.1	20.0	21.0
M2	15.9	17.8	23.6	24.3
M3	16.4	16.6	22.6	23.2

entostyles are weak or absent (cited by Webb [1983a] as a diagnostic feature of *P. hamiltoni*); M3 paracone-protocone and metacone-hypocone widths equal, contrasting *P. hamiltoni* in which the M3 paracone-protocone width is greater than that of the metacone-hypocone (also cited by Webb [1983a] as a diagnostic feature of *P. hamiltoni*). The quantitative differences between the upper dentition of Moss Acres Racetrack *Pediomeryx hemphillensis* and *P. hamiltoni* are even more striking than the morphological ones, as shown in Table 6-3. Every tooth of *P. hemphillensis* is clearly far smaller than its counterpart in *P. hamiltoni*. In addition distinct differences in length to width proportion are apparent in certain teeth of these of taxa, though this variation is not necessarily significant; proportional differences of this nature and magnitude have been observed in a large sample of teeth from an undescribed deer from the Bone Valley region of Florida (unpublished observations).

The lower dentition of Moss Acres Racetrack *Pediomeryx* is represented by two mandibles, UF 69945 and UF 97267, and an isolated lower incisor, UF 113565 (Figure 6-3). Measurements of these teeth are presented in Table 6-4. *Pediomeryx hemphillensis* was first described by Stirton (1936) on the basis of a lower mandible with cheek teeth, and the referral of the Moss Acres Racetrack *Pediomeryx* to *P. hemphillensis* is based on qualitative comparison of the Moss Acres Racetrack lower cheek tooth dentition with illustrations of *P. hemphillensis* dentition in Stirton (1936)

Table 6-4. Comparative measurements (millimeters) of *Pediomeryx hemphillensis* lower dentition from Moss Acres Racetrack (mandibles UF 69945 and UF 97267) and assorted sites, and *P. hamiltoni* from Love Bone Bed (all values for non-Moss Acres Racetrack specimens taken from Webb [1983]).

	P. hemphillensis					*P. hamiltoni*
tooth	UF 69945	UF 97267	Guy.	C.R.	M.E.	Love
P2						
length		8.1	8.4	8.3	8.3	11.1
width		5.7	4.6	6.2	5.3	6.8
P3						
length	9.6	11.5	13.1	12.9	11.8	14.1
width	7.2	9.2	7.7	10.0	7.2	9.3
P4						
length	*10.7	13.2	14.8	14.9	12.8	16.3
width	8.1	11.0	9.8	10.2	7.7	11.3
M1						
length	*11.2	16.7	17.8	15.6		20.2
width	11.5	10.9	12.5	12.7		15.0
M2						
length	16.2	19.5	21.4	20.4		23.1
width	13.0	12.9	14.1	13.2		16.3
M3						
length	22.6	23.9	29.7	28.5		32.5
width	11.9	11.4	14.3	12.6		16.2

* specimen shortened by intradental wear

abbreviations: Guy.= Guymon locality specimen, C.R.= Coffee Ranch locality specimen average, M.E.= Mount Eden locality specimen.

and Dahlquest (1983) and quantitative comparison with measurements of *P. hemphillensis* published in Webb (1983a). In neither qualitative nor quantitative features did the Moss Acres Racetrack *Pediomeryx* material differ significantly from *P. hemphillensis* material described in the literature. A comparison of Moss Acres Racetrack *Pediomeryx* with *P. hamiltoni* reveals the following. The p2 is small relative to the p3 in *P. hemphillensis* rather than nearly equal as in *P. hamiltoni*. The protoconid on the p4 is more constricted in *P. hemphillensis* than in *P. hamiltoni*. The m1 and m2 are very similar in these two species, contrary to Webb (1983a) who claimed that in *P. hemphillensis* the metaconid and entoconid of m1 and m2 enclosed the protoconid and hypoconid; examination of the unworn m1 and m2 of UF 97267 shows that these cuspids are without doubt distinct from each other. The m3 of *P. hemphillensis* differs from that of *P. hamiltoni* in lacking a posterolingual stylid (as noted by Webb, 1983a). The m3 heel varies considerably within both *P. hamiltoni* and *P. hemphillensis*; the heel of the M3 of UF 69945 is distinctly rounded with an internal enamel lake, while that of UF 97267 is more constricted and elongated without a lake (the m3 figured by Stirton [1936] for the *P. hemphillensis* specimen UCMP 30703 has a heel similar to that of UF 97267). The heel shape of *P. hamiltoni* varies similarly, though a lake is always absent (Webb, 1983a). All three incisors and the canine are preserved on the largely complete mandible UF 69945. A free incisor, UF 113565, has also been collected.

All of the incisors are gracile, being slender and narrow, and extend from their alveoli at approximately a 30 degree angle. They become progressively narrower from the i1 to the i3, with the canine narrower than the i3. The incisors and canines are unknown for P. hamiltoni.

Post-cranial Elements

Two partially complete, associated limbs of Pediomeryx have been recovered from Moss Acres Racetrack. The specimen UF 69946 consists of three proximal phalanges, three medial phalanges, one ungual phalanx, one highly pathological phalanx of uncertain position, one humerus proximal end, one radius distal end, one metapodial distal end, one tibia, and one femur distal end. The specimen UF 97266 consists of four proximal phalanges, four medial phalanges, four ungual phalanges, four assorted sesmoids, one distal femoral end and one broken femoral ball, one intact metapodial and one distal metapodial end, one tibia, one astragalus, one calcaneum, one cubo-navicular, and one patella. Measurements are presented in Table 6-5.

The Paleobiological Significance of Body Size Trends in Pediomeryx

In terms of their basic morphology, the two Pediomeryx subgenera P. (Yumaceras) and P. (Pediomeryx) are on the whole quite similar; neither shows significant qualitative differences that suggest these taxa occupied substantially different adaptive niches. However, they are strikingly

Table 6-5. Measurements (millimeters) of Moss Acres Racetrack *Pediomeryx hemphillensis* postcranial elements, UF 69946 and UF 97266.

UF 69946

- femur, right, distal end
  - width across condyles: 58.9
- tibia, right,
  - length: 240.0
  - mediolateral width across the distal articulating surface: 38.9
  - mediolateral width across the proximal articulating surface: 62.3
  - anteroposterior width across the distal articulating surface: 28.9
- partial metatarsal
  - proximal width: 35.3
- proximal phalanx
  - length: 44.9
- medial phalanx
  - length: 29.3
- distal (ungual) phalanx
  - length: 37.0

UF 97266

- femur, right, distal end
  - width across condyles: 55.6
- tibia, right
  - length: 240.0
  - mediolateral width across the distal articulating surface: 38.9
  - mediolateral width across the proximal articulating surface: 62.3
  - anteroposterior width across the distal articulating surface: 29.3
  - anteroposterior width across the proximal articulating surface: 64.9
- astragalus, right
  - length: 47.2
  - proximal width: 26.5
  - distal width: 28.0
- calcaneum, right
  - maximum length: 95.4
  - tuber width: 20.0
  - tuber height: 27.2
- cubonavicular, left
- metatarsal
  - length: 231.1
  - proximal width: 33.0
  - distal width: 33.5

different in terms of their size, the older *P*. (*Yumaceras*) being far larger than its younger cousin *P*. (*Pediomeryx*). Body size is an extremely important factor in a mammal's ecology, influencing the size of food items consumed, the quality of food items consumed, digestive efficiency, home range, and so on (Eisenberg, 1981; Owen-Smith, 1988; Jarman and Sinclair, 1979; see chapter 10). Thus despite their overall similarity, there must have been significant ecological differences between these two taxa. Current biochronological knowledge suggests an ancestor-descendent relationship between *P*. (*Yumaceras*) and *P*. (*Pediomeryx*) (Webb, 1983a); thus, the decrease in size from *P*. (*Yumaceras*) to *P*. (*Pediomeryx*) suggests an adaptational response to changing environmental conditions.

This change in *Pediomeryx* body size is especially significant in the context of the ungulate community of North America during the late Miocene. North America reached its peak ungulate diversity from the Barstovian to the middle or late Clarendonian, corresponding with a broad expanse of savanna that covered much of the continent. However these savannas were gradually replaced by open grasslands during the late Clarendonian or perhaps earliest Hemphillian and ungulate diversity decreased accordingly, with a particularly severe decrease between the late early Hemphillian and late Hemphillian (Webb, 1977; see chapter 10). *Pediomeryx* (*Pediomeryx*) replaced *P*. (*Yumaceras*) at an ecologically interesting time, immediately before the middle Hemphillian crash in ungulate diversity (Webb, 1983), and the question arises whether the decrease in size in Pediomeryx can be causally linked to a decrease in savanna habitat and a corresponding spread of steppe-like grassland.

Before answering this question, one must know something about the presumed feeding habits of Pediomeryx, i.e. whether it was a browser, grazer, or mixed feeder. On the basis of their deer-like dentition (i.e. brachyodont molars and poorly molarized premolars) the dromomerycids as a whole are generally considered to have been browsers, while the gracile incisors and slender mandibular symphysis of Pediomeryx specifically suggest a browsing diet in this animal (see above and chapter 10). In addition, Webb (1983b) observed a molar volume in Pediomeryx consistent with browsing (see chapter 10). Thus, Pediomeryx can be assigned to the browsing guild with fair confidence.

Within mammalian herbivores, all other factors being equal the quality of food consumed tends to be inversely proportionate to body size, with large herbivores able tolerate a poorer quality (i.e. more fibrous and difficult to digest) diet than small ones (see chapter 10 for a detailed discussion of this phenomenon). Thus small herbivores tend to seek out higher quality and generally scattered forage such as tender dicotyledonous leaves, though there are probable exceptions among some dwarf equid lineages like Nannippus (Owen-Smith, 1988; Prothero and Sereno, 1982;

Jarman and Sinclair, 1979; Webb and Hulbert, 1986; see chapter 10).

Consider a browser facing the situation of woodland savanna with its relative abundance of trees being replaced by open grassland. In a broad evolutionary sense the browser has two possible strategies for survival: it must either sustain itself on the more scattered, overall less abundant browse offered in the less common woodland pockets, or else find a way to utilize the abundant but nutritionally poor grass of the newly formed grass. Webb (1983a) proposed that unlike the typically browsing dromomerycids *Pediomeryx* fed on both browse and grass, based on its possession of more hypsodont teeth and a deeper mandibular ramus than typical for dromomerycids, and thus followed the the second of the two aforementioned strategies. If *Pediomeryx* was indeed a mixed feeder that evolved from a browsing cranioceratine dromomerycid, than one would expect to see a distinct phylogenetic trend towards increasing body size in this lineage with the spread of the grasslands, since poor fodder quality is always correlated with relatively large body size in living ruminants. Such a trend is visible within the cranioceratine dromomerycids as a whole, culminating with *P.* (*Yumaceras*) (Webb, 1983a), and this trend could be interpreted as indicating that poor quality fodder, presumably grass, was incrementally becoming a more important component of the diet within the cranioceratine lineage. However, when the savannas of North America were largely replaced by pure grassland in the early Hemphillian, Pediomeryx actually underwent a major body size reduction, decreasing its relative mandibular depth and thus becoming even more brachyodont than before. This is an unlikely response by a ruminant to a coaser, poorer quality diet.

With increased grazing shown to be an implausible basis for explaining the decrease in body size in Pediomeryx, one might be tempted to rule out diet as a causal factor altogether and look for a different explanation for this situation. However, it is possible to invoke diet as an explanation for this change if one assumes that Pediomeryx was actually evolving into a more specialized browser rather than a more generalized mixed-feeder. Within ungulates dwarfism is generally (though not universally) associated with isolated, usually island, environments, examples including elephants, a hippopotamus (Phanourios), and the key deer of the Florida Keys. While the ecological basis for this trend is unclear, it has been suggested that dwarfism may allow more efficient use of a limited quantity of quality food (Prothero and Sereno, 1982). In the context of food resources, woodland pockets in the restricted Hemphillian savannas can be thought of as ecologically equivalent to islands for Pediomeryx if one assumes that its populations were hindered in dispersing among the pockets by the intervening expanses of grassland. Thus, Pediomeryx may represent an example of continental "island" dwarfing. Another possible example of such dwarfing may lie in dwarf populations of the rhinoceratids Peraceras and Teleoceras on the Gulf Coastal Plain of Texas, possibly related to restricted endemicism within forests of this region (Prothero and Sereno, 1982). However, perhaps the best modern analog to this situation is the duikers. Janis (1986) proposed that the duikers are ruminants whose ancestors subsisted on a relatively poor quality diet but subsequently evolved into animals specialized for browsing on succulent leaves in enclosed woodlands.

CHAPTER 7
THE PALEOECOLOGY OF *APHELOPS MUTILIS* (PERISSODACTYLA, RHINOCERATIDAE) IN THE MOSS ACRES RACETRACK FAUNA

The rhinoceros *Aphelops mutilis* is by far the most abundant species in the Moss Acres Racetrack fauna in terms of identified specimens, represented by 77 and rivaled only by *Alligator* sp. with 47 referred specimens (a list of the *Aphelops* specimens in the Moss Acres Racetrack fauna is presented in Appendix 3; see Appendix 4 for a list of *Alligator* specimens) This abundance indicates that *Aphelops* was an important, perhaps dominant member of the site's terrestrial community. The possible role of *Aphelops* in the Moss Acres Racetrack paleocommunity is discussed in detail in chapter 10. However, before one can examine an organism's role in a community one must first understand its ecology as an individual. Thus the autecology of *Aphelops* is discussed here, including a simple analysis this animal's population ecology, possible behavioral ecology, and feeding behavior.

Systematics

Order Perissodactyla

Family Rhinoceratidae

Aphelops Cope, 1873

Aphelops mutilis Matthew, 1924

Aphelops is one of two rhinoceratid genera known from North America during the late Miocene (Clarendonian-Hemphillian), the other being *Teleoceras*. *Aphelops* is diagnosed as follows: skull medium to long with high, narrow occiput; nasals hornless, slender, decurved, and shortened; cheek teeth moderately brachyodont to subhypsodont; premolars unreduced, roughly equaling the molars in size; on the cheek teeth accessory crests not greatly developed, crochet present, antecrochet poorly developed or absent, transverse valleys usually open; upper incisors vestigial or absent, lower incisor tusks less curved than *Teloceras*, wearing to form subtle facets; and limbs of normal rhinoceratid proportions or slightly elongate (Bennett, 1977; Matthew, 1932). The rhinoceratid material from Moss Acres Racetrack agrees well with this diagnosis, allowing it to be confidently referred to *Aphelops*.

The referral of this *Aphelops* material to species is a more difficult matter. Three species of *Aphelops* are well known from the late Clarendonian through the late Hemphillian: *A. malacorhinus*, *A. kimballensis*, and *A. mutilis*. A referral of the Moss Acres Racetrack material to *Aphelops kimballensis* can be discounted on the basis of two characters: a body size significantly smaller than *A. kimballensis* (but similar to *A. malacorhinus*; see Table 7-1); and the presence of a p2, absent from *A. kimballensis* (but shared with *A. malacorhinus*) (Bennett, 1977; Tanner, 1967). A referral to *Aphelops malacorhinus* can also be discounted,

Table 7-1. Cranial and dental measurements (millimeters) of selected *Aphelops* cranio-dental specimens.

UF 97265, partial disassociated skull (Moss Acres Racetrack)
occipital height: 270
nasals
length: 126 minimum basal width: 82

UF 116844, skull (Moss Acres Racetrack)
P2
antero-posterior length: 53 medio-lateral width: 36
P3
antero-posterior length: 56 medio-lateral width: 42
P4
antero-posterior length: 60 medio-lateral width: 54
M1
antero-posterior length: 62 medio-lateral width: 53
M2
antero-posterior length: 60 medio-lateral width: 50
M3
antero-posterior length: 44 medio-lateral width: 43

UF 116845, skull (*Aphelops mutilis*, Moss Acres Racetrack)
total toothrow length (P1-M3): 281
P1
antero-posterior length: 20 medio-lateral width: 19
M1
antero-posterior length: 62 medio-lateral width: 53
M2
antero-posterior length: 60 medio-lateral width: 50
M3
antero-posterior length: 40 medio-lateral width: 47

UF 36428, skull (*Aphelops malacorhinus*, Love)
nasal
length: 170 minimum basal width: 99
tooth row length (P1-M3): 280
P1
antero-posterior length: 23 medio-lateral width: 23
P2
antero-posterior length: 42 medio-lateral width: 45
P3
antero-posterior length: 46 medio-lateral width: 54
P4
antero-posterior length: 51 medio-lateral width: 59
M1
antero-posterior length: 53 medio-lateral width: 56
M2
antero-posterior length: 61 medio-lateral width: 50

Table 7-1--continued

M3
antero-posterior length: 52 medio-lateral width: 45

UF 135803, mandible (male, *Aphelops mutilis*, Moss Acres Racetrack)
length (tusk-condyle): 603
tooth row length (p2-m3): 292
ramus depth (at m1): 89
p2
antero-posterior length: 41 medio-lateral width: 27
p3
antero-posterior length: 45 medio-lateral width: 30
p4
antero-posterior length: 47 medio-lateral width: 33
m1
antero-posterior length: 52 medio-lateral width: 34
m2
antero-posterior length: 55 medio-lateral width: 32
m3
antero-posterior length: 49 medio-lateral width: 27

UF 103713, mandible (male, *Aphelops mutilis*, Moss Acres Racetrack)
tooth row length (p2-m3): 286
ramus depth (at m1): 131
p2
antero-posterior length: 38 medio-lateral width: 25
p3
antero-posterior length: 47 medio-lateral width: 32
p4
antero-posterior length: 48 medio-lateral width: 31
m1
antero-posterior length: 49 medio-lateral width: 28
m2
antero-posterior length: 50 medio-lateral width: 31
m3
antero-posterior length: 50 medio-lateral width: 26

UF 103714, mandible (female, *Aphelops mutilis*, Moss Acres Racetrack)
tooth row length (p2-m3): 298
ramus depth (at m1): 110*
p2
antero-posterior length: 33 medio-lateral width: 24
p3
antero-posterior length: 43 medio-lateral width: 30
p4
antero-posterior length: 44 medio-lateral width: 30
m1
antero-posterior length: 54 medio-lateral width: 30

Table 7-1--continued

m2
antero-posterior length: 54   medio-lateral width: 28
m3
antero-posterior length: 52   medio-lateral width: 27

UF 97265, mandible (*Aphelops mutilis*, Moss Acres Racetrack)
dp4
antero-posterior length: 43   medio-lateral width: 25
m1
antero-posterior length: 49   medio-lateral width: 29
m2
antero-posterior length: 52   medio-lateral width: 28

UF 24728, mandible (male, *Aphelops malacorhinus*, McGeehee)
length (tusk-condyle): 612
tooth row length (p2-m3): 273
ramus depth (at m1): 114
p2
antero-posterior length: 35   medio-lateral width: 24
p3
antero-posterior length: 43   medio-lateral width: 29
p4
antero-posterior length: 45   medio-lateral width: 30
m1
antero-posterior length: 51   medio-lateral width: 32
m2
antero-posterior length: 52   medio-lateral width: 29
m3
antero-posterior length: 50   medio-lateral width: 29

despite the similarity demonstrated above, on the basis of three characters: significantly more reduced nasals than in *A. malacorhinus* (see Table 7-1); an antecrochet present on the cheek teeth, absent from *A. malacorhinus* (but present in *A. kimballensis*); and a crochet on the upper molariform cheek teeth that closely approaches or completely merges with the metaloph, contrasting *A malacorhinus* whose crochet remains distinctly separate (Bennett, 1977). Other *Aphelops* species exist in the literature (e.g., *A. megalodus*), but these are either considerably smaller than the Moss Acres Racetrack animal or else are poorly known (Bennett, 1977; Cope, 1873). Thus, a referral to *Aphelops mutilis* is most plausible.

Osteology

The osteology of *Aphelops mutilis* will not be discussed in detail here, as this taxon is well known from a number of well studied late early to late Hemphillian localities (e.g., Coffee Ranch [Dahlquest, 1983] and Rhinoceros Hill [Bennett, 1977]). However measurements of selected cranial and post-cranial elements from the Moss Acres Racetrack fauna are presented in Tables 7-1 and 7-2, accompanied in some cases by measurements of *Aphelops kimballensis* and/or *A. malacorhinus* specimens for comparative purposes.

Population Ecology

The *Aphelops* assemblage from Moss Acres Racetrack represents a clear (though not necessarily synchronous)

Table 7-2. Measurements (millimeters) of selected *Aphelops mutilis* post-cranial elements from Moss Acres Racetrack.

UF 97265, scapula
length: 363
width at posterior ramus border:
diameter of glenoid fossa:

UF 90300, humerus
length: 380
maximum diameter of head: 85
width across trochlea: 99
width across head and greater tubercle: 135
minimum medio-lateral shaft width: 53

UF 90300, radius
length: 327
width across proximal articulation surface: 91
width across distal articulation surface: 82
minimum medio-lateral shaft width: 46

UF 90300, ulna (olceranon process broken)
length from top of sigmoid notch-proximal end: 370

UF 118542, metacarpal II
length: 146
width across distal articulation surface: 37

UF 118542, metacarpal III (distal end broken)
minimum length: 173

pelvis, UF 135828
maximum width across ileum: 447
maximum diameter of acetabulum: 94
maximum length from ileum to pubic symphysis: 467
maximum length from ileum to ischium: 488
length from dorsal acetabulum margin to medial ischium: 249

UF 69977, femur
length from ball to medial condyle: 526
width from ball to greater trochanter: 218
width across condyles: 113
width across epicondyles: 80

Table 7-2--continued

UF 69977, tibia
length: 356
medio-lateral width across proximal articulation surface: 119
antero-posterior length across proximal articulation surface: 112
medio-lateral width across distal articulation surface: 106
antero-posterior length across distal articulation surface: 65
minimum medio-lateral shaft diameter: 61

UF 69977, fibula
length: 297
antero-posterior length across proximal head: 51
minimum antero-posterior shaft diameter: 21

UF 69977, astragalus
medio-lateral width of tibial articulation surface: 75
maximum antero-posterior length: 68
width of navicular articulation surface: 66

UF 93467, calcaneum
maximum antero-posterior length: 113
tuber length: 85
maximum width across astragalar articulation surface: 77

UF 93467, metatarsal II
length: 133
width across distal articulation surface: 34

UF 93467, metatarsal III
length: 154
width across distal articulation surface: 37

UF 93467, metatarsal IV
length: 143
width across distal articulation surface: 47

UF 93467, metatarsal V
length: 134
width across distal articulation surface: 32

population, containing significant numbers of both juveniles and adults. Thus it can be subjected to an analysis of its population ecology, a useful prerequisite for understanding other aspects of this animal's autecology and community ecology.

An important step in analysing the population ecology of an organism is determining the number of individuals in the population, a difficult task when fossil organisms are involved. In studies of fossil vertebrate assemblages where skeletal dissociation in most cases obscures the true number of individuals represented, the minimum number of individuals (MNI) concept is normally invoked (e.g., Voorhies, 1969). In order to determine the MNI for a given species in a fossil assemblage the elements that represent single individuals (e.g., left astragali, right M3's, and so on) are counted, with the count of the most abundant element defined as the MNI. For the Moss Acres Racetrack Aphelops population the MNI is set at nine, a value derived independently from both the number of skulls and mandibles (see Appendix 3).

One aspect of population ecology amenable to study for assemblages of fossil organisms is age structure. Previous studies have examined the age structures of certain fossil mammal populations in detail, allowing survivorship curves for age classes to be calculated from measurements of cheek tooth wear and replacement stages (e.g., Voorhies, 1969 [Merycodus furcatus]; Hulbert, 1982 [Neohipparion]). However, such analyses require tooth sample sizes in the hundreds to be statistically meaningful (e.g., 475 for *Merycodus furcatus* in Voorhies [1969]), making an analysis at this level impossible for the Moss Acres Racetrack *Aphelops* population. Nevertheless the sample size is sufficient for a crude analysis of age structure, allowing the proportion of adults to nonadults (i.e., juveniles) in the population to be estimated.

Before beginning even a crude analysis of population age structure, one must set criteria for assigning individuals to age categories. At a gross level adult mammals can be distinguished from juveniles on the basis of their dental ontogeny, the dentition of adults consisting solely of permanent teeth while that of juveniles consists of permanent and/or deciduous teeth. Most of the *Aphelops* dentition recovered from Moss Acres Racetrack is associated with skulls and mandibles, the bases for estimating the MNI, rather than isolated teeth. Thus, the estimate of the proportion of adults to juveniles in the Moss Acres Racetrack *Aphelops* population can be conveniently connected to the MNI estimate.

Aphelops skulls and mandibles with deciduous dentitions, representing juvenile individuals as defined here, are presented in Table 7-3. From the four specimens listed, a minimum of three juvenile individuals can be inferred based on differences in their ontogenetic sequences: UF 69943, UF 97265, and UF 115633/UF 115635 (the skull UF 115633 and the mandible UF 115635 are tentatively considered to represent a single individual because of their ontogenetic similarity,

Table 7-3. Dentititions of juvenile *Aphelops mutilis* individuals from the Moss Acres Racetrack site.

UF 69943, skull: dP1-dP4, M1, M2 erupting

UF 97265, skull and mandibles: dP1, P2, dp4, m1-m2, m3 erupting

UF 115633, skull*: dP1, P2, dP3-dP4, M1-M3

UF 115635, mandible*: di3, p2-p3, dp4, m1-m3

*: considered a possible single individual based on a similarity in dental ontogenetic sequence

the upper and lower dental ontogenies of individuals not necessarily being in complete synchrony). Thus with an MNI for the fossil population of nine and a minimum of three juvenile individuals, the proportion of juveniles in the Moss Acres Racetrack *Aphelops* population can be estimated to be at least 0.33. It should be noted however that roughness aside this estimate may only poorly reflect the actual juvenile proportion of the original *Aphelops* population, preservational conditions having possibly introduced significant biases either for or against the survival of juvenile remains (in most cases juveniles are strongly underrepresented in fossil assemblages [Behrensmeyer et. al., 1992; see chapter 9 for a detailed discussion of fossil preservation]). Nevertheless, this estimate is sufficient to show that juveniles must have formed a significant component of the Moss Acres Racetrack *Aphelops* population. This is hardly a surprising finding considering that this animal must have taken years to reach adulthood (the the juveniles of the modern white rhinoceros of Africa, *Ceratotherium simum*, normally do not cease nursing until they are over a year old), had a long gestation period (greater than a year; see below), and had a significant length of time between breedings (at least a year apart) by virtue of its large body size (Eisenberg, 1981; Owen-Smith, 1988), requiring a fair number of juveniles to be present at any one time for the population to be reasonably stable.

The juvenile component of a fossil assemblage can also be used to estimate age class mortality (e.g., Voorhies, 1969; Hulbert, 1982). A first glance at this crude *Aphelops* data might lead one to infer that juveniles had a lower mortality rate than adults based on their lower numbers, but this inference can be considered suspect for two reasons. First, as mentioned above juveniles tend to be underrepresented in fossil assemblages, implying that juvenile mortality rates observed in fossil assemblages (even large ones) are probably underestimates. And secondly, preservational biases aside the Moss Acres Racetrack *Aphelops* sample is too small for any inferences drawn from it to be statistically meaningful. The white rhinoceros, a possible modern analog of *Aphelops* (see below), has relatively low annual mortality rates throughout most of its lifespan, with a value of less than eight percent for juveniles and typically three percent or less for adults (Owen-Smith, 1988). Some preliminary research on the *Aphelops malacorhinus* population from the Love site suggests that this animal had juvenile mortality rates similar to those of the black rhinoceros (*Diceros bicornis*), which in turn are roughly comparable to those observed for the white rhinoceros (Webb, 1983b; Owen-Smith, 1988).

Though juveniles are reliably represented only by three individuals, it is tempting to investigate whether their individual ontogenetic dental sequences might suggest additional information about the *Aphelops* population, the sequences indicating the relative age of the individuals. None of the specimens represent likely neonates (identified by nearly or completely unworn fully deciduous dentition) and thus there is no evidence that Aphelops females actually gave birth at Moss Acres Racetrack, though this possibility cannot be ruled out. Based on the reasonable assumption that the fewer the number of permanent cheek teeth (or conversely the more deciduous cheek teeth) the younger the individual, the Moss Acres Racetrack juveniles can be placed in the following order from youngest to oldest: UF 69943 (M2 erupting, dP1-dP4 present), UF 97265 (m3 erupting, dP1 and dP4 present), and UF 115633/UF 115635 (M3/m3 erupted, dP4/dp4 and dP1 present). Both the individuals UF 97265 and UF 115633/UF 115635 are clearly close in age, and conceivably represent a distinct age class (assuming significant individual variation in the timing of the dental ontogenetic sequence); indeed, if UF 115633 and UF 115635 actually represent different individuals, then three of the four juveniles in the fossil fauna belong to a single age class. A tendency for Aphelops individuals to belong to discrete age classes without intermediate ontogenetic stages would strongly imply that this animal gave birth seasonally and/or that this animal was only present at the site seasonally (Hulbert, 1982), though the aforementioned evidence is sufficent only to suggest this possibility due to the extremely small sample size (see chapter 10). It should be noted however that there are theoretical reasons to be suspicious of age classes in

Aphelops. Both the modern white and black rhinoceros calve aseasonally due in part to their long gestation periods (419-479 days for the black rhinoceros, and 480-550 days for the white rhinoceros [Nowak and Paradiso, 1983]). The gestation length of a mammal tends to be strongly correlated with its body mass (Eisenberg, 1981). Since Aphelops had a body mass very roughly similar to that of the black and white rhinoceroses (estimated at 764 kg, see chapter 10) its gestation length must have been greater than a year as well, and thus it must have calved aseasonally. If this reasoning is correct, than the suggested age classes in the Moss Acres Racetrack Aphelops juveniles must be considered the result of a statistical aberration rather than biological reality.

Social Structure

The social structure of mammals tends to be reflected in their morphology, particularly in regards to sexual dimorphism or its lack thereof. Dimorphism in size (i.e., quantitative dimorphisim) or specific morphological features such as horns and canines (i.e., qualititative dimorphism) provides clues to such behavioral aspects as whether a given species was monogamous or polygynous, territorial or non-territorial among others (Janis, 1986; Eisenberg, 1981; MacFadden, 1993).

Aphelops possesses no dimorphic skull features that allow males to be distinguished from the females, and hence in Table 7-1 individual skulls are not identified to sex.

Aphelops mandibles in contrast show strong dimorphism in their incisor tusks, presumed males having much larger tusks than females with a distinctive lateral flare, though they are well developed in both sexes (Dalquest, 1983). Of the _Aphelops_ mandibles recovered from Moss Acres Racetrack, three can be identified as males and one as a female (see Appendix 3 and Table 7-1). Measurements of the one female and the two well preserved male mandibles are presented in Table 7-1, and an examination of these measurements reveals that the female compares favorably in size with the males, indeed being distinctly larger than the males in some respects such as tooth row length (Dalquest [1983] also failed to note any quantitative sexual dimorphism in a study of the abundant _Aphelops_ material from the Coffee Ranch fauna). Thus overall quantitative sexual dimorphism in _Aphelops_ cranial features can be discounted, though a subtle quantitative dimorphism may exist, requiring a statistical analysis of a larger sample size than that available from Moss Acres Racetrack to be detected.

As noted above the lower incisor tusks of _Aphelops_ are distinctly dimorphic, though they are of respectable size in both sexes. The relative development of tusks in males and females of a given species relates to their usefulness in both procuring food and/or their social function (Lambert, 1992). There is no evidence that the tusks of _Aphelops_ were used significantly during feeding (see below); thus, their relative development must relate to social function in some fashion.

Such large, visible dimorphic features as tusks and cranial appendages (i.e., "horns") are used in mammals both to make threat displays (e.g., canine-baring in babboons) and in direct combat (e.g., antler-locking in cervids). In some cases the structures may serve both roles; for example, cervid males may use their antlers to intimidate less endowed rivals, and engage in combat only against males with racks of similar stature (Attenborough, 1990). It would appear based on their enlarged tusks that at least the Aphelops males were organized into a social hierarchy, presumably structured on the basis of tusk size and/or combat skill. Though there is no direct evidence to support it, in all likelihood this hierarchy was centered on access to breeding females, presumably dominant males having struggled through display and/or combat to maintain sole or primary access to one or more receptive females. What is not immediately clear however is the exact social nature of these interactions, e.g. whether the males defended territories that females entered of their own accord (a strategy practiced by the white rhinoceros[Owen-Smith, 1988]) or whether a harem was defended as in some modern equids (MacFadden, 1992).

Jarman (1974) examined the relationship between the social behavior of modern African antelopes and their horn development, and observed that the greatest sexual dimorphism is found in those species in which the male is relatively sedentary and defends a territory. Those antelopes that have to search considerably for particularly high quality morsels (e.g., small taxa like duikers) and thus do not defend a territory tend to have poorly developed horns, while those that wander widely while grazing (e.g., the wildebeest) tend to have sexes with equally developed horns. Thus, at least in antelopes strong horn dimorphism is a product of territoriality. Aphelops is not an antelope, and is dimorphic in its tusks rather than horns (a keratinous horn was absent from this animal as indicated by the complete lack of an attatchment scar on the nasals). However, Jarman's reasoning can be extrapolated to Aphelops if caution is used. Assuming that the tusks of Aphelops actually were fighting weapons analogous to horns (and indeed, tusks are used in this fashion in the living Indian rhinoceros [Owen-Smith, 1984]), their sexual dimorphism suggests that Aphelops males were territorial, and thus at least moderately sedentary as opposed to migratory like the wildebeest. Nevertheless one interesting fact to be considered is that this dimorphism is not as extreme as that seen in such strongly dimorphic antelopes as the kudu (Tragelaphus), both sexes possessing well developed tusks. In some cases, such weak dimorphism is the result of the dimorphic feature being important for acquiring some important resource such as food (e.g., the tusks of the African elephant [Lambert, 1992]). However as discussed below, there is no evidence that these tusks were used for feeding or digging. The tusks could have also been used as weapons against predators, though with the one possible exception of the false sabercat *Barbourofelis* there were no known predators in the late Miocene of North America large enough to have tackled an adult *Aphelops*. It is conceivable that the tusks were used in threat displays and/or as weapons against conspecifics by females as well as males; for example, female Indian rhinoceroses are intolerant of other females, reacting aggressively during encounters (Owen-Smith, 1984). Finally, following Jarman's antelope model, this situation may actually be the result of a loss of territoriality in the *Aphelops* males, a lack of dimorphism in well developed horns characterizing non-territorial antelopes. (If this latter hypothesis is correct, then one would predict that progressively older *Aphelops* species will show greater tusk dimorphism; however, there is no evidence for such increased dimorphism in the late Clarendonian/early Hemphillian species *Aphelops malacorhinus*).

The evidence indicates that the sexual dimorphism observed in *Aphelops* is most plausibly explained by male territoriality, presumably governing access to females. The presence of well developed tusks in the females further suggests that the females may also have been territorial. If such dual territoriality actually existed, it would indicate that the social organization of *Aphelops* differed considerably from the normal pattern observed in modern ungulates. In either case territoriality in *Aphelops* indicates that this animal was sedentary, or at least did not migrate in a systematic fashion. The ramifications of this behavior for the Moss Acres Racetrack community are discussed in chapter 10.

Diet and Feeding Mode

There is some controversy regarding the general diet of *Aphelops*, *Aphelops* having been considered to be both a browser (e.g. Leite, 1990) and a grazer (e.g. Webb, 1983b). Evidence in favor of a browsing diet is as follows: its cheek are teeth distinctly low-crowned (brachyodont to subhypsodont at best), apparently poorly suited for withstanding an abrasive diet; its mandibular symphysis is strongly tapered, more suited for taking selective bites of vegetation rather than the large indiscriminate bites normally required for grazing (see chapter 10 for a detailed discussion of this subject); and it has no obvious cropping mechanism, anterior incisiform teeth such as found in extant grazing artiodactyls and equids being absent. Webb (1983b) however identified *Apelops* as a grazer on the basis of a plot of largest molar total volume versus estimated body mass for various late Miocene ungulates as opposed to simple crown height (see below).

None of these lines of evidence are conclusive. For example, the modern *Hippopotamus* is a grazing specialist despite having brachyodont, bunodont molars while the strongly hypsodont modern pronghorn *Antilocapra* browses considerably (Nowak and Paradiso, 1983; Hulbert, 1993).

Moreover, though a grazing specialist *Ceratotherium* has a distinctly narrow and tapered mandible like *Aphelops*. *Ceratotherium* also resembles *Aphelops* and differs from typical grazers in lacking incisiform teeth for cropping, grass being torn by this animal primarily by its powerful, flexible upper lip (Nowak and Paradiso, 1983). Resolving this ambiguity about the diet of *Aphelops* requires two lines of evidence to be evaluated: 1) Webb (1983b)'s plot of molar volume versus body mass, and 2) the plausibility of *Ceratotherium* as an analog for *Aphelops*.

In seeking to assign late Miocene ungulates into their appropriate feeding guilds Webb (1983b) examined the relationship between log body mass and molar volume, molar volume chosen over simple hypsodonty by virtue of its greater indication of the potential functional longevity of the tooth (the m1 alone was utilized in the study in order to simplify both measurement and calculation). These data were plotted for entire ungulate faunas, and trends within the plots examined. Using a plot of the modern Serengeti ungulate fauna as a control Webb observed a pattern related to guild membership, browsers and mixed-feeders/grazers (these two categories being difficult to separate) occupying different portions of the distribution with the grazers and showing a distinct linear relationship (Figure 7-1). Similar distributions were observed for plots of late Miocene ungulate faunas, and Webb assigned feeding guilds to the taxa

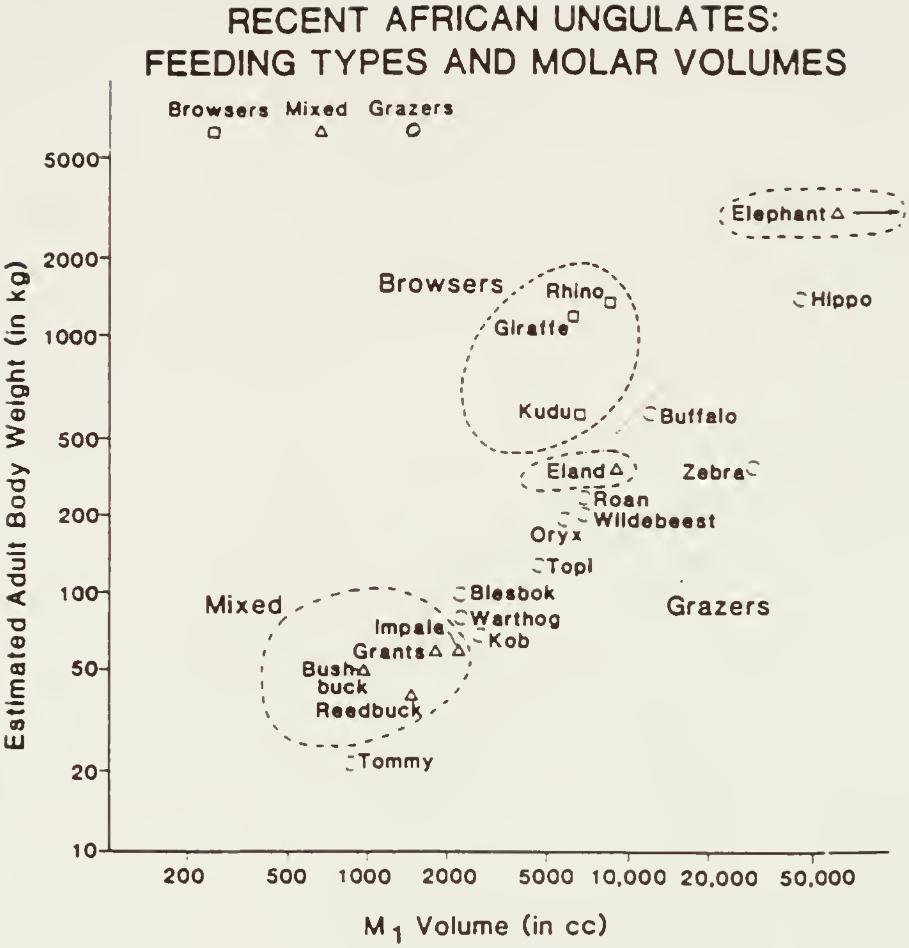

Figure 7-1. Plot of estimated body masses versus m1 volume for Recent African ungulate taxa showing feeding categories (taken from Webb [1983b]).

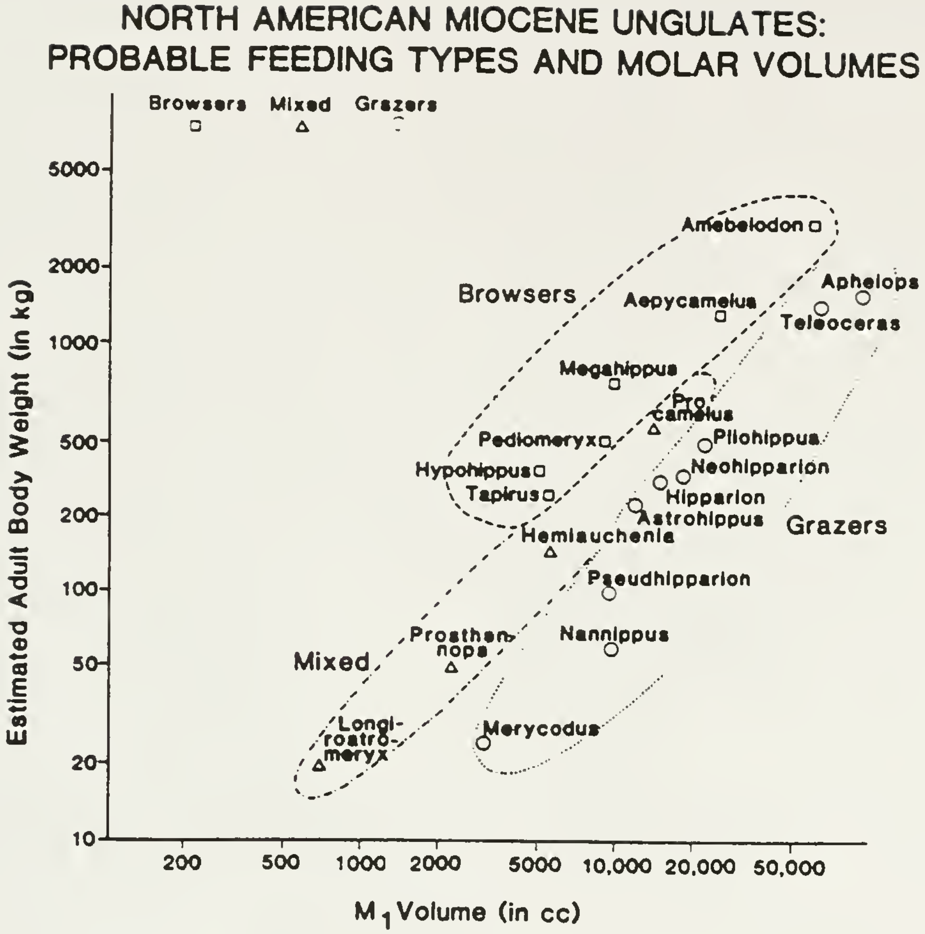

Figure 7-2. Plot of estimated body masses versus m1 volume for Miocene North American ungulate taxa showing feeding categories (taken from Webb [1983b]).

on the basis of their location within the distribution (Figure 7-2).

Potential difficulties with Webb's methodology are as follows. First, body mass is difficult to estimate for extinct taxa (see chapter 10) and significant errors could conceivably shift taxa considerably within the distribution, causing their guilds to be misidentified. However, an examination of the data in Figure 7-1A shows that error in molar volume would have a greater impact on guild identification than body mass, a feature not prone to major measurement error in fossil mammals. Furthermore, the significance of errors in body mass estimate that do occur is reduced by the fact that the plot is based not on mass but rather log mass, which minimizes the impact of all but gross misestimates. Another, possibly more serious problem with Webb's analysis lies in the potential difficulty of distinguishing mixed-feeders from browsers and grazers, particularly when they lie near the boundary of these categories. For example, the eland (Taurotragus) in Figure 7-1 is a mixed feeder that is at once directly within the broad grazer line, yet very close to the browsers; thus it would be difficult to identify this animal's feeding guild without additional information. Similarly the mixed-feeders in the cluster near the left bottom of the grazer line would be impossible to confidently assign to a guild. Thus this plot shows only limited usefulness in placing modern ungulates into their proper feeding guilds, though it does appear to reliably isolate browsers.

Other factors however support the reliability of Webb's methodology. For example in Figure 7-1 Hippopotamus is correctly identified as a grazer, though its bunodont dentition suggests that it should be a browser or at most a mixed-feeder. Teleoceras, a rhinoceros commonly considered to be the ecological equivalent of a hippopotamus and a demonstrated grazer (see Webb 1983B), is correctly identified as a grazer in Figure 7-2 and indeed is plotted in almost the same exact location as the hippopotamus in Figure 7-1. Thus, this methodology appears to have a significant degree of predictive reliability in at least these two cases. Since Aphelops occupies a position in Figure 7-2 a considerable distance from the browsers, the likelihood that it is a misidentified mixed-feeder is small. Thus, Webb's identification of Aphelops as a grazer must be considered to be at least plausible, if tentative.

Webb's identification aside it is necessary to demonstrate that Aphelops was actually capable of grazing, since it has morphological features that conflict with those seen in normal ungulate grazers and would appear to have made grazing difficult. The plausibility of Aphelops as a grazer hinges in large part on its likely functional similarity to Ceratotherium, a grazing rhinoceros with unusual features similar to those observed in Aphelops (see above). If Ceratotherium is to serve as a reasonable model for a grazing

Aphelops then two facts must be established: 1) that *Aphelops* had the capacity for taking large bites of grass despite its narrow mandible; and 2) that its upper lip was well developed like that of *Ceratotherium*, strong and flexible enough to tear grass in the absence of incisiform dentition.

In examining the question of *Aphelops*' ability to take large bites of grass, the ventral maxillary profiles of three other rhinoceros taxa were examined: *Diceros* (browser, from the mammal collection of the Florida Museum of Natural History), *Rhinoceros* (browser, figure from Lawlor, 1979), and *Teleoceras* (grazer, various Love site specimens) (no *Diceratherium* specimens or illustrations were available for examination). A surprising feature of the four rhinoceroses examined (including *Aphelops*) is the uniformity of their ventral maxillary profiles. The known grazer *Teleoceras* is essentially indistinguishable in this respect from the modern browsing taxa *Diceros* and *Rhinoceros* as well as the unknown *Aphelops*, a contradiction to the pattern observed in equids and artiodactyls. One must conclude from these findings that either rhinoceroses tend to take the same sized bites irrespective of their diet, or more reasonably that some other factor than anterior maxillary width regulates bite size in rhinoceroses.

The grazing *Ceratotherium* and its modern browsing relatives such as *Diceros* and *Rhinoceros* can be readily distinguished on the basis of their upper lip morphologies. The upper lip of *Ceratotherium* is distinctly broad and the animal's primary cropping device (see below). The upper lips of Diceros and Rhinoceros in contrast are relatively slender and flexible, suitable for selectively manipulating vegetation rather than taking indiscriminate bites (Owen-Smith, 1984). This pattern suggests that for rhinoceroses the upper lip is more important than maxilla shape in determining feeding behavior, and by implication that maxillary profile has no bearing on determining the diet of Aphelops.

The preceding hypothesis negating the significance of maxillary profile to the feeding behavior of Aphelops is based on the premise that Aphelops had an upper lip roughly similar to that of modern rhinoceroses, a premise whose validity is as of yet undemonstrated. At first glance it would appear difficult if not impossible to determine the development of the upper lip of Aphelops, since this structure is not directly preserved on the fossil skull (but see discussion of the possible relationship between upper lip flexibility and size of the dorsal preorbital fossa of equids in MacFadden [1992]). However indirect evidence for the nature of the Aphelops upper lip is preserved on its large lower incisor tusks. As noted by Dalquest (1983), the tusk-like lower incisors of Aphelops are characterized by shallow wear facets, essentially polished surfaces, on the proximal regions of their dorso-medial surfaces. On the Moss Acres Racetrack specimens the wear surfaces were equally developed on both right and left tusks. Food manipulation (e.g., vegetation cutting, rooting) can be ruled out as a likely source for these surfaces, since they show no sign of an edge (required for cutting vegetation) or wear on the tip (a necessary result of rooting and similar behavior) (see Lambert [1992] for a detailed discussion of tusk wear surfaces and feeding behavior). The most reasonable explanation for these wear surfaces is that they are the result of habitual contact with a well developed upper lip, similar surfaces on modern elephant tusks being known to form through continuous contact with the trunk (Eisenberg, pers. comm.). The exact nature of this upper lip, i.e. whether it is broad like that of *Ceratotherium* or relatively slender and flexible like those of *Diceros* and *Rhinoceros*, is unclear. However, the wear surfaces are separated by a great width (greater than the anterior width of the maxilla and premaxilla) and at least on the Moss Acres Racetrack specimens equally developed on the right and left side, suggesting that these tusks were uniformly worn by a broad lip rather than irregularly worn by a wandering slender lip. This evidence is inconclusive however, and one can say with fair assurance only that *Aphelops* had a well developed upper lip at least roughly similar to that found on modern rhinoceroses in general. (Bjork [1978] observed similar wear patterns on the lower tusks of the late Oligocene rhinoceros *Amphicaenopus*, and likewise interpreted them as the result of continuous wear from a well developed upper lip.)

Only one line of evidence points towards Aphelops having been a grazer, it position on Webb's body mass/molar volume plot. Ventral maxillary profile, useful in prediciting the feeding guild of artiodactyls and equids, evidently has little or no application to rhinoceroses while upper lip morphology and function, useful in distinguishing browsers from grazers among modern rhinoceroses, cannot be examined in sufficient detail in Aphelops to make an unquestioned determination of its feeding guild. These ambiguities aside however, it is noteworthy that no evidence has been found that argues against Aphelops having been a grazer. Since Webb's plot has been shown to have at least modest predictive reliability (see discussion of Hippopotamus and Teleoceras above), and since Aphelops occupies a region of this plot that is clearly separate from the browsers, a tentative identification of Aphelops as a grazer is not unreasonable. Nevertheless this identification may require reevaluation as new evidence becomes available.

CHAPTER 8

MISCELLANEOUS NON-MAMMMALIAN AND MAMMALIAN TAXA IN THE MOSS ACRES RACETRACK FAUNA

So far in this dissertation the mammal fauna of the site has been emphasized, the primary focus of this study, particularly taxa that were currently unstudied and well represented. However there are other important aspects of the fauna that must be addressed if the paleoecology of the site is to be analyzed: non-mammals, mammals that have been or are in the process of being studied by other workers, and mammals that are represented in the fauna by insufficient material to warrant a detailed study. Taxa belonging to these three categories are briefly discussed here, with the specimens listed in Appendices 3, 4 and 5. The Moss Acres Racetrack Local Fauna, including only those taxa that were part of the Hemphillian community as opposed to those secondarily introduced from older sediments via reworking (e.g., the various sharks; see below), is presented in Table 8-1.

Class Chondrichthyes

A few chondrichthyean specimens, including both sharks and rays, have been collected from Moss Acres Racetrack (see Appendix 3). Unlike any of the other specimens found at the

Table 8-1. The Moss Acres Racetrack Local Fauna.

- Class Osteichthyes
  - *Lepisosteus* sp.
- Class Reptilia
  - *Apalone* sp.
  - *Trachemys* sp.
  - *Pseudemys* sp.
  - *Alligator* sp.
- Class Aves
  - Family Anatidae (genus indeterminate)
- Class Mammalia
  - Order Carnivora
    - *Enhydritherium terraenovae*
    - *Osteoborus orc*
  - Order Xenarthra
    - *Pliometanastes* cf. *protistus*
  - Order Proboscidea
    - *Amebelodon* (*Konobelodon*) *britti*
  - Order Artiodactyla
    - Tayassuidae (genus indeterminate)
    - cf. *Aepycamelus*
    - *Hemiauchenia* sp.
    - New genus near *Pseudoceras* ("*Pseudoceras*")
    - *Pediomeryx hemphillensis*
    - Antilocapridae (genus indeterminate)
  - Order Perissodactyla
    - *Aphelops mutilis*
    - *Dinohippus* sp.
    - cf. *Astrohippus*
    - *Calippus mccartyi*
    - *Hipparion* cf. *tehonense*
    - *Nannippus aztecus*
    - *Nannippus morgani*
    - *Cormohipparion plicatile*
    - *Cormohipparion emslei*
    - *Neohipparion trampasense*

site, these are phosphatized and evidently reworked from adjacent limestone, presumably the phosphate-rich Hawthorn (see chapter 2).

Class Osteichthyes

Lepisosteus

The generic gar, Lepisosteus, is an ancient taxon in North America, extending from the late Cretaceous to the Recent (Carroll, 1988). It is currently largely restricted to the eastern half of the continent and the Neotropics, but was a common component of Great Plains faunas during the Miocene (Migdalski et al., 1983; Schultz, 1977). Four gar specimens are known from Moss Acres Racetrack, three isolated scales and one associated partial skeleton consisting of some vertebrae and scales. They do not differ significantly in appearance from typical late Cenozoic gars.

Class Amphibia

For unknown reasons amphibians are completely absent from Moss Acres Racetrack fauna. Presumably this is the result of a taphonomic bias rather than a true absence (see chapter 9).

Class Reptilia

Apalone cf. ferox

Traditionally the soft-shelled turtles of North America are referred to the genus Trionyx, an ancient genus extending back to the Cretaceous. However, a recent taxonomic study by Meylan (1987) led him revive the disused name *Apalone* and refer to it all North American *Trionyx* species, the name *Trionyx* being strictly reserved for Old World taxa.

Apalone is represented in the Moss Acres Racetrack fauna by a single specimen, an associated partial carapace and plastron. The posterior half of the Moss Acres Racetrack carapace resembles that of modern *Apalone ferox* (currently found in region), being considerably more constricted medio-laterally and more elongated antero-posteriorly than that of the extant species *A. spinniferus* (which currently has a more northerly distribution than *A. ferox*). However a major diagnostic feature for *Apalone ferox*, a fused hyoplastron and hypoplastron (Meylan, 1987), is not preserved in the Moss Acres Racetrack specimen so that a definite referral to species cannnot be made.

Pseudemys

The fossil record of the family Emydidae, the North American "pond turtles," extends back to the Eocene, with the group appearing in the oldest (Oligocene) terrestrial faunas of Florida (Carroll, 1988; Meylan, 1984). Some of the more prominent taxa in the group, *Chrysemys*, *Pseudemys*, and *Trachemys*, have been subject to taxonomic dispute, with some authors referring *Pseudemys* and *Trachemys* to *Chrysemys* as distinct subgenera, and others considering all three taxa to be valid genera (Rose and Weaver, 1966). The latter convention, utilized by Meylan (1984), is adopted here.

Pseudemys is an abundant animal in the Moss Acres Racetrack fauna, represented by 24 specimens including associated partial carapaces and plastrons (see Appendix 3). Unfortunately, despite its abundance and tendency towards association most of this material is badly fragmented, so that comparison with specimens from other sites is difficult. As far as comparison is possible Moss Acres Racetrack *Pseudemys* resembles the *Pseudemys* from the McGeehee site (early Hemphillian) in most respects, referred to *P. caelata* by Jackson (1977). However, these two animals differ considerably in their nuchal morphology (Figure 8-1). The nuchal of *P. caelata* has lateral flanges that are sharply tapered and symmetrical, as opposed to the shallowly tapered, asymmetrical lateral flanges of Moss Acres Racetrack *Pseudemys* (preserved, rather poorly, only on a single specimen, UF 69931). In addition, the posterior nuchal margin is much narrower in *P. caelata* than Moss Acres Racetrack *Pseudemys*. In both of these aspects Moss Acres Racetrack *Pseudemys* more closely resembles the living species *P. concinna* (the Suwannee cooter) than *P. caelata*, though the lateral flanges of *P. concinna* are more sharply tapered and the posterior margin less broad than in Moss Acres Racetrack *Pseudemys*. . The nuchal of Moss Acres Racetrack *Pseudemys* differs from those of both *P. caelata* and *P. concinna* in having a deeply cleft anterior margin.

Considering the distinctiveness of its nuchal morphology (an important feature in emydid turtle systematics, e.g. Rose and Weaver, 1966), the possibility exists that the Moss Acres Racetrack *Pseudemys* represents a new species. It is noteworthy that the *Pseudemys* from the Withlacoochee River 4A site, approximately the same age as and in close proximity to Moss Acres Racetrack, is indistinguishable from *P. caelata*. Thus, it is unlikely that the possible new species from Moss Acres Racetrack is a chronospecies anagetically derived from *P. caelata*.

Trachemys

Trachemys is known on the basis of two associated specimens, a partial carapace and a partial skeleton including carapace and plastron elements (see Appendix 3). The carapaces of both specimens display the strong wrinkled sculpturing diagnostic for the genus. *Trachemys* is known in the literature from faunas that are latest Hemphillian in age and younger (Weaver and Robertson, 1967). Thus, the Moss Acres Racetrack *Trachemys* may represent the oldest record for the genus.

Geochelone

Geochelone, a tortoise, is a relatively old genus in North America, extending back to the Eocene, and is a common element of both Great Plains and Gulf Coastal Plain faunas during the Miocene (Carroll, 1984; Schultz, 1977).

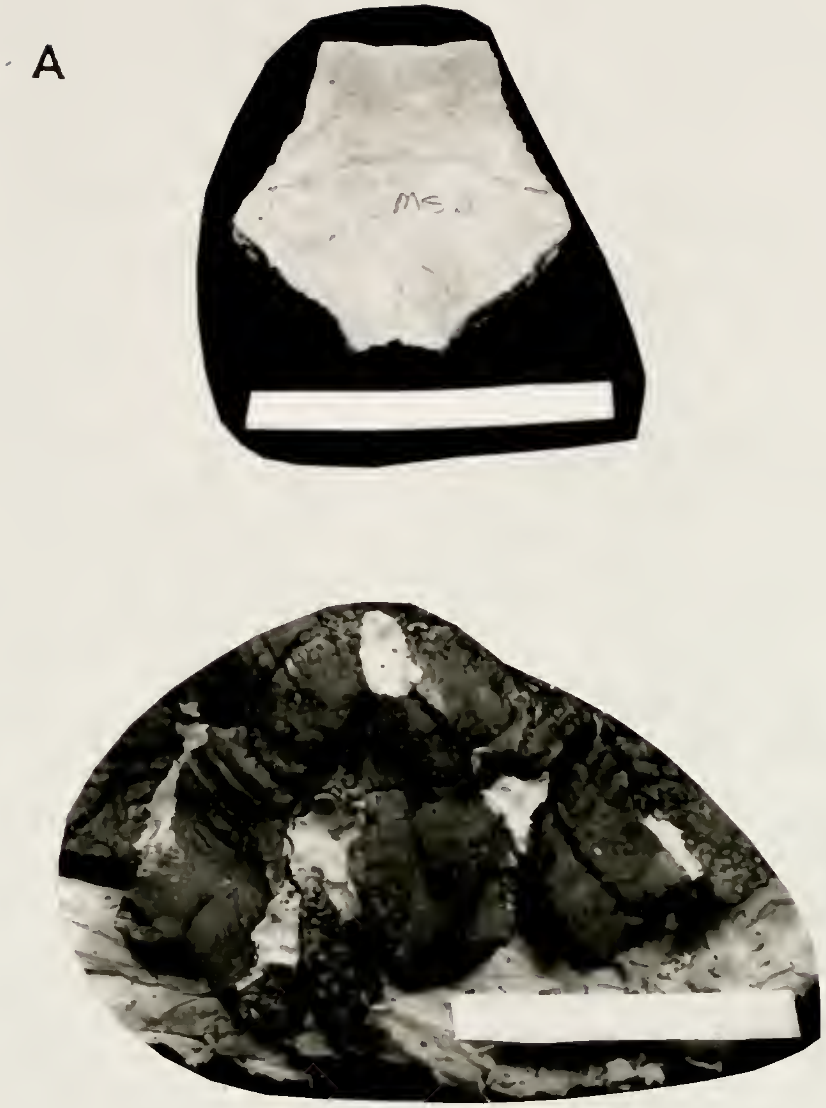

Figure 8-1. nuchals of Pseudemys (scale bar represents five centimeters). A) Pseudemys caelata from the McGeehee site (uncatalogued specimen); B) UF 69931, Pseudemys sp. from Moss Acres Racetrack site.

Geochelone is represented in the Moss Acres Racetrack fauna by a single specimen, a small hyoplastron.

Alligator

The record of *Alligator* in North America goes back to the Oligocene, and it first appeared in Florida during the Hemingfordian (late early Miocene). Tertiary *Alligator* material has been poorly studied but two species are generally recognized in the literature, *A. olseni* and *A. mississippiensis* (Auffenberg, 1967; Meylan, 1984).

Alligator sp., along with *Aphelops mutilis*, is one of the most abundant species in the Moss Acres Racetrack fauna, represented by 47 specimens including nearly complete skeletons as well as intact, associated skulls and mandibles (see Appendix 3). The species represented is unclear. The Moss Acres Racetrack skulls were compared with skulls of both modern *Alligator mississippiensis* and a cast of a skull of *A. olseni* (the type specimen, MCZ 1887) (see cranial measurements in Table 8-2). The Moss Acres Racetrack skulls differ from those of the other two alligators in having frontals that are strongly sculptured and deeply concave with distinct lateral ridges, as well as significantly narrower upper temporal fenestrae (Figure 8-2). The Moss Acres Racetrack *Alligator* falls in the size range of living *A. mississippiensis* and is considerably larger than *A. olseni*; *A. olseni* seldom exceeded eight feet in length (Auffenberg, 1967), while one Moss Acres Racetrack specimen has been

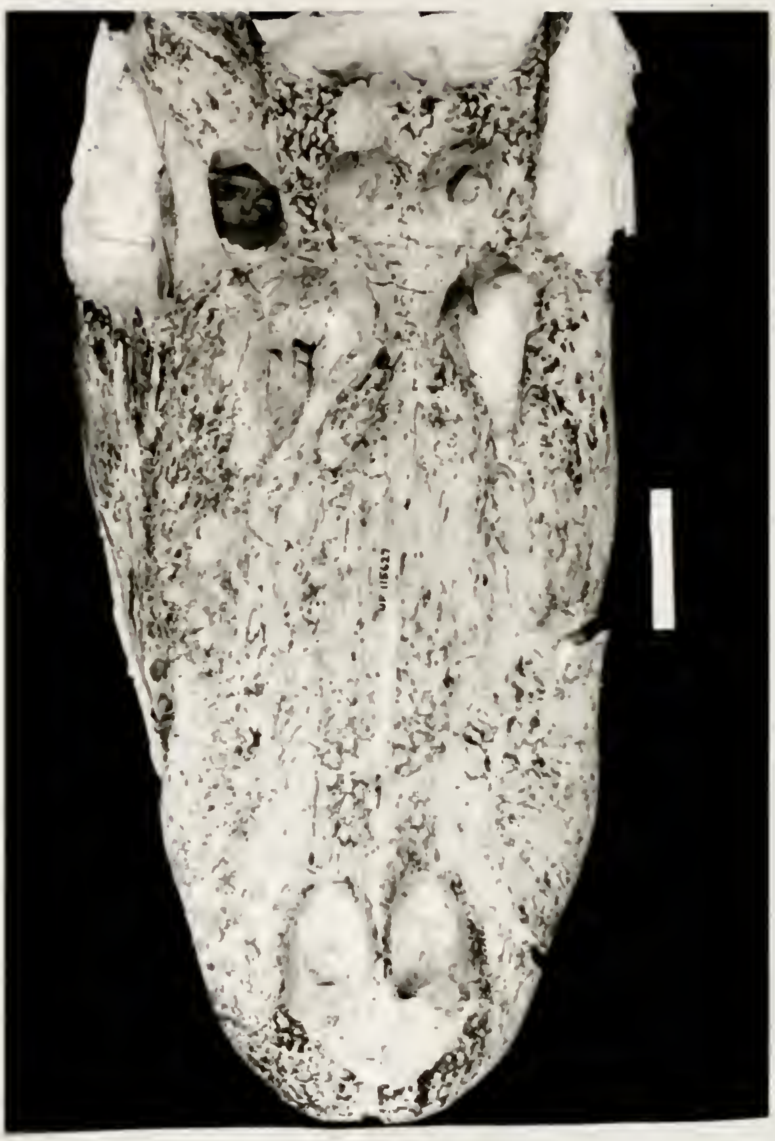

Figure 8-2. Skull of Alligator sp. from Moss Acres Racetrack (scale bar represents five centimeters).

Table 8-2. Measurements (millimeters) of selected miscellaneous non-mammal and mammal specimens from Moss Acres Racetrack in the collection of the Florida Museum of Natural History.

Alligator sp.
Skull, UF 95427
length from occipital condyle to premaxilla: 437
snout width at anterior orbital border: 219
width across quadrates: 224
width across retroarticular processes: 198

Skull, UF 115627
length from occipital condyle to premaxilla: 357
snout width at anterior orbital border: 165
premaxilla width: 101

Osteoborus orc
cuboid, UF 69948
antero-posterior length: 18
proximal articulation width: 11
distal articulation width: 11

metacarpals III-V, UF 104244
III
length: 54
minimum shaft width: 7
maximum width across proximal articulation surface: 10
maximum width across distal articulation surface: 9
IV
length: 54
minimum shaft width: 7
maximum width across proximal articulation surface: 11
maximum width across distal articulation surface: 9
V
length: 45
minimum shaft width: 7
maximum width across proximal articulation surface: 7
maximum width across distal articulation surface: 10

Camelidae, genus indeterminate
proximal half of proximal phalanx, UF 69949
width across proximal articulation surface: 23
minimum shaft width: 12

proximal half of proximal phalanx, UF 69950
width across proximal articulation surface: 25

astragalus, UF 104242
length: 57
width: 40

Table 8-1--continued

cf. *Aepycamelus*
cervical vertebra, UF 115630
centrum length: 347
width across zygopophyses: 81
minimum centrum width: 58

new genus near *Pseudoceras*
distal articulating surface of tibia, UF 95402
width: 15

Antilocapridae, genus indeterminate
astragalus, UF 116848
length: 34
width: 22

estimated by Vliet (pers. comm.) to have been eleven feet long. On the basis of these differences from *Alligator mississippiensis* and *A. olseni*, Vliet (pers. comm.) has suggested that the Moss Acres Racetrack *Alligator* may represent a new species.

Class Aves

Birds are represented in the fauna by only two specimens, a single partial coracoid, identified as that of a duck (family Anatidae) by Emslie, and an unidentifiable shaft of a limb bone.

Class Mammalia

Osteoborus orc Webb, 1969

Terrestrial carnivores in the Moss Acres Racetrack fauna are directly represented by a mere two specimens, a set of three associated canid metacarpals and an isolated canid cuboid (see Appendix 4). The metacarpals are referred to *Osteoborus* based on an overall resemblance to *Osteoborus galushai* from the McGeehee site, though the Moss Acres Racetrack specimens are considerably smaller and more slender, particularly in their articulating surfaces (see measurements in Table 8-2). In their general proportions the Moss Acres Racetrack metacarpals resemble *Osteoborus orc* from the Withlacoochee River 4A site, though there are no metacarpals in this fauna with which to make a direct comparison, and this specimen is tentatively referred to this species. The cuboid is clearly that of a canid, and has proportions consistent with Osteoborus orc (no Osteoborus cuboids could be found for direct comparison) (see Table 8-2). Thus, this element is tentatively referred to this species as well.

Osteoborus orc is unusual both biogeographically and biochronologically, being currently known from two sites, Moss Acres Racetrack and the Withlacoochee River 4A. Both are in close proximity and approximately the same age, early late Hemphillian (see chapters 2 and 10). This taxon, as well as the similarly restricted Calippus mccartyi and Nannippus morgani (see below) may reflect a significant level of faunal endemicism in Florida during this time.

Order Sirenia, Genus Indeterminate

A single, heavily water-worn sirenian rib fragment has been recovered from Moss Acres Racetrack. The absence of water wear from all other vertebrate specimens found in the site (see chapter 9), and the absence of in situ marine vertebrates from the fauna indicate that this specimen has been reworked from adjacent limestone along with the shark and ray teeth (see above).

Family Tayassuidae, Genus Indeterminate

Peccaries are represented in Moss Acres Racetrack by only a single partial deciduous premolar, referrable to this family on the basis of its bunodont morphology.

Family Camelidae, Genus Indeterminate

A significant amount of small camelid material has been recovered from Moss Acres Racetrack, morphologically unidentifiable and plausibly referrable to either Hemiauchenia or Procamelus on the basis of size. Both taxa were present during the early Hemphillian (Schultz, 1977).

Hemiauchenia Cope, 1893

A single cuneiform, UF 93464, is referred to Hemiauchenia on the basis of a strong morphological similarity to Hemiauchenia minima from the Love site..The cuneiform of this genus is easily distinguished from that of Procamelus on the basis of its more complex, diagnostic articulation surfaces. The Moss Acres Racetrack Hemiauchenia cuneiform is significantly larger than that of H. minima and probably represents a different species, perhaps H. vera (see Table
8-2).

cf. Aepycamelus

A single large, elongated cervical vertebra of a camelid has been recovered from Moss Acres Racetrack representing a long-necked, giraffe-like camel (see measurements in Table 8-2). Two genera are known in this category from the early Hemphillian, Aepycamelus and Megatylopus (Schultz, 1977). Comparison with Aepycamelus from the Love site reveals a strong similarity, and this specimen is tentatively referred to this genus rather than *Megatylopus*.

New Genus (Near *Pseudoceras*) and Species

A distal articulating surface of a small artiodactyl tibia has been recovered from Moss Acres Racetrack. This specimen is indistinguishable in both size and morphology from a *Pseudoceras*-like animal from the Withlacoochee River 4A site (see Table 8-1 for measurement), an undescribed new genus and species (see Webb, 1969). Like *Osteoborus orc* this animal may represent a taxon endemic to the Florida late early Hemphillian, though the Withlacoochee River 4A material must be properly described before this can be verified.

Family Antilocapridae, Genus Indeterminate

This family is represented in the fauna by a single specimen, a rodent-gnawed astragalus. It is morphologically indistinguishable from modern *Antilocapra*, both animals sharing a relatively large calcaneal facet and a broad, shallow ridge in the tibial groove.

Family Equidae

The horses comprise an enormous portion of the Moss Acres Racetrack fauna, encompassing 120 specimens including a number of partial skeletons and numerous associated limb elements (see Appendix 5). The Moss Acres Racetrack horses have been and are currently being studied by Richard Hulbert of Georgia Southern University. Thus they will not be studied in depth here, but only summarized. Horse identifications to the level of genus or below were mostly made by either Richard Hulbert or Gary Morgan. The equid classification scheme used follows that of Hulbert (1992). Equid dental terminology is explained in Figure 8-3, and equid specimens in the Moss Acres Racetrack fauna are presented in Appendix 5.

Family Equidae, Tribe and genus indeterminate

A large amount of horse material unidentifiable to the tribal level (see below) has been recovered from Moss Acres Racetrack, mostly limb material (both isolated and associated specimens). Based on their relatively small size, the majority of these specimens are plausibly referrable to tridactyl taxa.

Family Equidae, Tribe Equini

The equinine equids have the following diagnosis: dorsal preorbital fossa moderate in depth, with a shallow posterior pocket; protocone-protoloph connection present even during weak wear stages on P3 and P4; hypoconid lake on p3 and p4; metastylid on the p3-m2 much smaller than the metaconid; metastylid on p3 and p4 located more lingually than the metaconid, and more labially on the m1 and m2. This group includes both tridactyl (e.g., *Calippus*, *Protohippus*,) and monodactyl (e.g., *Dinohippus*, *Equus*) forms (MacFadden, 1992). Of the equine specimens from Moss Acres Racetrack one has not

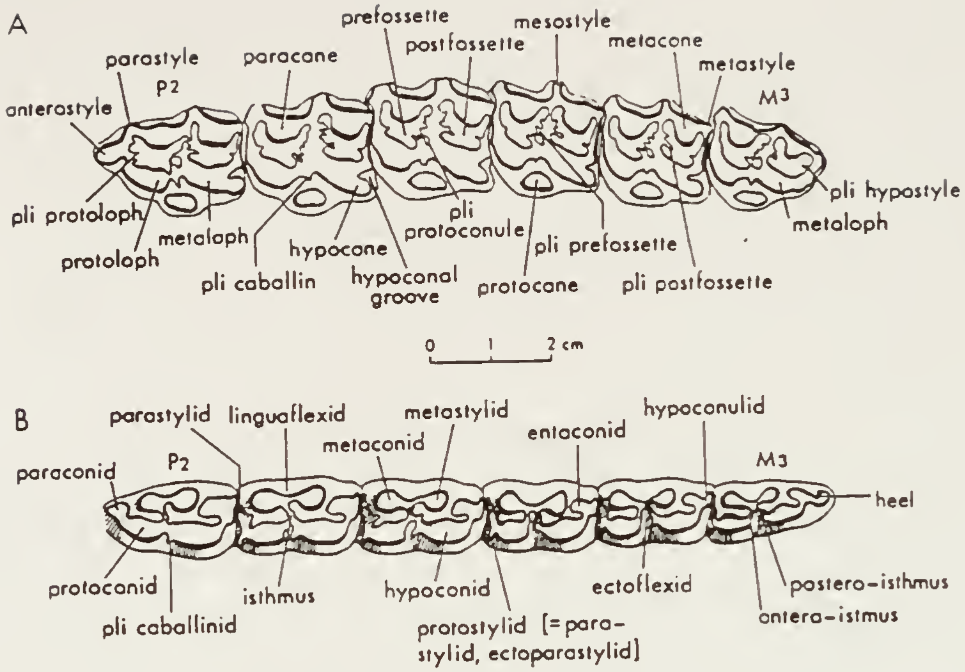

Figure 8-3. Illustration demonstrating equid dental terminology utilized in this paper (taken from MacFadden [1984]). A) upper dentition; B) lower dentition.

been specifically identified to genus, having been tentatively referred to a large monodactyl horse such as *Astrohippus* or *Dinohippus*.

Cf. *Astrohippus* Stirton, 1940

The associated forelimb of a large monodactyl horse (UF 97270) was tentatively referred to the genus *Astrohippus* by Hulbert. The post-cranials of *Dinohippus* and *Astrohippus* are difficult to distinguish (MacFadden, 1986), and the basis for this referral is not clear, though size may have been a factor.

Dinohippus Quinn, 1955

Like *Astrohippus*, *Dinohippus* is a large monodactyl horse, commonly considered to be close to the ancestry of *Equus*. Its dentition is very similar to that of *Equus*, with *Dinohippus* and primitive *Equus* being potentially confusible in some cases (MacFadden, 1986). The skull of *Dinohippus* can be distinguished from those of *Astrohippus* and *Pliohippus* by its more poorly developed dorsal preorbital fossa, a feature that is nearly or completely absent from *Equus* (MacFadden, 1992).

The Moss Acres Racetrack *Dinohippus* material consists of three specimens, two of them juvenile, including a skull (unfortunately the skull is does not preserve the dorsal preorbital fossa). The M2 differs from that of ordinary

Dinohippus in being strongly medio-laterally curved, a feature more typical of Pliohippus (Morgan, pers. comm.).

Calippus Matthew and Stirton, 1930

Unlike Astrohippus and Dinohippus, Calippus is a tridactyl form. Its most prominent diagnostic features are its unusual muzzle shape and anterior dentition; the muzzle is expanded anteriorly, while I1-I2/i1-i2 are especially broad and positioned so as to form upper and lower straight rows of four teeth (contrasting more typical grazing equids, in which these rows are distinctly curved), with I3/i3 sharply angled posteriorly. This feature is interpreted as an adaptation for taking particularly large mouthfuls of grass (see chapter 10). Other, less conspicuous diagnostic characters of Calippus include: dorsal preorbital fossa long and relatively shallow; cheek teeth moderately to extremely hypsodont (i.e., high-crowned); upper cheek teeth with an oval or elongated protocone broadly connected to the protoloph, simple fossettes generally lacking plications, and simple pli caballins that are stronger on the premolars than the molars; lower cheek teeth with typically non-persistent lingual flexids, shallow premolar ectoflexids, and lacking plications and pli caballinids; and deciduous lower premolars lacking ectostylids (Hulbert, 1988a). Of the Calippus material known from Moss Acres Racetrack three isolated specimens, including two juveniles, have been identified by Hulbert as Calippus without referral to species.

Calippus mccartyi Hulbert, 1988a

This species was described by Hulbert (1988a) based on a study of material from both the Moss Acres Racetrck and Withlacoochee River 4A sites, with the designated holotype, UF 69951 (an associated partial skull and mandible) from Moss Acres Racetrack. This species is diagnosed on the basis of cheek tooth morphology: preprotoconal groove deep and persistent; protocone elongate; lingual border of cheek teeth rounded to slightly flattened, oriented silghtly obliquely; hypoconal groove open until mid-wear, forming lakes on P2-P4; pli caballin small and single, vestigial or absent from molars; plications simple but persistent throughout wear; upper cheek teeth not as curved as in other *Calippus* species; lower cheek teeth with widely expanded metaconids and metastylids; lingual flexids more persistent than in other species; and ectoflexid shallow on p2-p4, only moderately deep on m1-m3 (Hulbert, 1988a). *Calippus mccartyi* is represented from Moss Acres Racetrack by a poorly preserved skull, a mandible, and eight free cheek teeth, of which only two (UF 95408, a P3 and P4) are associated. Like *Osteoborus orc*, *Calippus mccartyi* is biogeographically and biochronologically highly restricted, known only from the late early Hemphillian Moss Acres Racetrack and the Withlacoochee River 4A sites.

Family Equidae, Tribe Hipparionini

The hipparionine equids are commonly diagnosed by a protocone that is isolated from the protoloph, though this character may vary in extremely worn teeth and in primitive taxa within this clade. Another character that distinguishes this group is a well developed and consistent pli caballin on the molars. All hipparionines are tridactyl (MacFadden, 1992).

Hipparion de Christol, 1832

Hipparion is a complex taxon, and the reader is referred to MacFadden (1984) for an in depth systematic discussion of this genus.

Hipparion cf. H. tehonense Merriam, 1916

Hulbert (1988b) tentatively referred two Moss Acres Racetrack equid cheek teeth, an M3 and m2, to Hipparion tehonense on the following bases. The M3 is in the same size range as Cormohipparion ingenuum and Neohipparion trampasense, but resembles Hipparion in having a shorter, oval protocone, simple fossette plications, and a weak pli caballin. The m2 resembles Hipparion in having a deep ectoflexid, no pli caballinid, and no isthmus plications. The Moss Acres Racetrack specimens are closer in size to H. tehonense than H. forcei, the only two advanced species of Hipparion recognized in North America.

Nannippus Matthew, 1926

Nannippus is a small, gracile hipparionine with hypsodont to very hypsodont teeth. Its diagnosis is as follows: rostrum relatively elongated; post-canine diastema wide; dorsal preorbital fossa absent; upper cheek teeth with oval protocones and moderately complex plications on the fossette borders; lower cheek teeth with deep ectoflexids; pli caballinids vestigial or absent; metastylids and metaconids widely separated; p2 with the anterior extension of the paralophid small; and metapodials relatively slender and elongate (MacFadden, 1984).

Nannippus aztecus Mooser, 1968(= *N. minor* Sellards, 1916)

Nannippus aztecus is a particularly small species of *Nannippus*, though not the smallest (see below). It is diagnosed by a small cheek tooth occlusal area, well developed protostylids, and extremely small and relatively elongated metapodials (MacFadden, 1984).

Nannippus aztecus is the best represented identifiable equid in the Moss Acres Racetrack fauna. It is known from both a skeleton (UF 69933/69934) and an abundance of both associated and isolated dental and post-cranial elements, including juvenile individuals.

Nannippus morgani Hulbert, 1993b

This species is considerably smaller than *Nannippus aztecus* (see chapter 10), and is the the smallest hipparionine equid yet discovered. Beyond its size, it is diagnosed by a persistently open and deep hypoconal groove, unreduced molar hypocone, elongate to oval protocone with a spur absent or rudimentary, pli caballins, pli caballinids, and protostylids well developed, and a shallow ectoflexid. It is rare in the Moss Acres Racetrack fauna, represented by only an M1 and a metatarsal. Besides Moss Acres Racetrack this species is known only from the Withlacoochee River 4A site, where it is more common. Like *Osteoborus orc* and *Calippus mccartyi*, this species may be a late early Hemphillian Florida endemic (Hulbert, 1993b).

Cormohipparion Skinner and MacFadden, 1977

Cormohipparion is a medium to large equid, with mesodont to hypsodont cheek teeth. Its most outstanding diagnostic character is its dorsal preorbital fossa, which has the following features: prominent, with well developed anterior and posterior rims (the posterior rim being pocketed), oval or teardrop shaped, and extending far forward on the cheek. Other less prominent diagnostic characters include: anterior margin of the lacrimal posterior to the posterior margin of the dorsal preorbital fossa; protocone rounded with an anterior spur; fossette borders moderately to highly plicated; protostylids usually present and moderately developed; ectoflexids moderate to deep, and pli caballinids moderate to absent (MacFadden, 1984). A partial skeleton lacking dentition and an unworn upper molar have been identified as *Cormohipparion* by Hulbert without referral to species.

Cormohipparion (*Notiocradohipparion*) Hulbert, 1988c

This subgenus of *Cormohipparion* is primarily diagnosed by an elongated post-canine diastema, presumably a specialization for grazing on grass of a particular height or a particular bite size (see chapter 10) (Hulbert, 1988c).

Cormohipparion emslei Hulbert, 1988b

Cormohipparion emslei is a small to medium-sized, moderately hypsodont species of *Cormohipparion*. Its diagnosis is as follows: protocone relatively small, oval to elongate in shape with flattened or concave lingual borders (rounder on P2), remaining isolated from the protoloph except with extreme wear; fossette plications more complex and pli caballinid better developed than in any other North American *Cormohipparion* species; parastyle of P3 and P3 grooved, occasionally also M1 and M2; metastyle present, often relatively prominent; ectoflexid shallow, not penetrating the isthmus on p2-p4; metaconid and metastylid of dp2-dp4 and p2-p4 with lingual groove in early wear stages; metaconid and paraconid of dp2 and p2 frequently connected in moderate wear stages, isolating the metaflexid as a fossetid.

Cormohipparion emslei is known from Moss Acres Racetrack on the basis of both adult and juvenile material. The mandible of a female individual (sexed on the basis of the absence of canines), UF 92759, was closely associated in the field with the specimen UF 97260, an associated upper and lower dentition consisting only of relatively unworn deciduous incisors and premolars, and the possibility that these two specimens represent an association between a mother and a fetus or neonate cannot be ruled out.

Cormohipparion plicatile Leidy, 1887

Cormohipparion plicatile is a medium-sized *Cormohipparion* species, on average smaller than *C. occidentale*, larger than *C. ingenuum* and *C. emslei* (but see chapter 10). Its diagnois is as follows: fossettes less complicated, and protocone and diastema less elongated than in *C. occidentale*; fossette plications more complex than in *C. sphenodus* and less complex than in *C. enslei*; and pli caballinid weaker than in *C. emslei* (Hulbert, 1988c).

Cormohipparion plicatile is well represented in the Moss Acres Racetrack fauna, including the skeleton of a juvenile individual and two well preserved, associated adult mandibles. One mandible, UF 103754 (figured in Hulbert [1988c]), exemplifies the wide diastema that characterizes the subgenus *C.* (*Notiocradohipparion*).

Neohipparion Gidley, 1903

Neohipparion is a medium to large-sized hipparionine, moderately to very hypsodont. Like *Cormohipparion*, it is primarily diagnosed on the basis of its dorsal preorbital fossa, which is poorly developed or absent, the anterior portion (if present) developed on the nasal and maxillary bones and fading into the surrounding facial area, and the posterior portion developed on the nasal, maxillary, and sometimes the lacrimal (commonly lacking a well developed rim or pocket). In addition, its upper cheek teeth protocones are very elongate,and its metapodials moderately to very elongate (MacFadden, 1984).

Neohipparion trampasense Edwards, 1982

Neohipparion trampasense is diagnosed as follows: dorsal preorbital fossa rudimentary if not absent; protocones with angular borders; fossette borders relatively plicated; pli caballinid and isthmus well developed on the lower premolars; pli caballinid well developed and ectoflexid deep in the lower molars; isthmuses frequently plicated (MacFadden, 1984). This species is represented in the Moss Acres Racetrack fauna by three relatively well preserved mandibles.

CHAPTER 9
THE TAPHONOMY OF THE MOSS ACRES RACETRACK SITE

The geology and fauna of the Moss Acres Racetrack site have been described in chapters 2 through 8. With this background we can now explore the local conditions at the site that resulted in vertebrates being preserved there, and possible faunal biases created by those conditions.

Taphonomy, a subdiscipline of paleontology, has been given a number of different definitions, though all center on the process of fossil preservation. Efremov (1940), who originated the term taphonomy, defined it as the study of the total process of burial, involving all aspects of the transfering organic remains from biosphere to lithosphere including both biological and physical factors. Many subsequent authors have altered this definition somewhat. For example, Raup and Stanley (1978) defined taphonomy as the process of information loss manifested in fossil preservation, while Laporte (1979) defined taphonomy as all the events and processes that affect organisms from the time of their death until their discovery as fossils. Taphonomic analyses are important in reconstructing the original ecosystem in which a fossil biota lived. Loosely following these definitions, this taphonomic analysis of the fossils from Moss Acres Racetrack will address the following questions. 1) What were the conditions that led to the preservation of vertebrate bones found at the site; 2) what was the paleohabitat when the preserved animals lived there (a question also addressed in chapter 2); and 3) what preservational biases exist in the fossil fauna of the site?

Data

When the Moss Acres Racetrack site was first worked from 1985-1987, no taphonomic data (e.g., relative position, depth, orientation, and plunge of specimens) were taken. Thus, when the site was reopened in the spring of 1991 under controlled circumstances, gathering taphonomic data was a primary goal.

In order to measure the position of any fossil, one must have a local fixed point of reference (the only alternative is to use absolute global coordinates, clearly an impractical proposition for objects separated by distances on a scale of centimeters or at most meters). To satisfy this requirement, a permanent pole was positioned at a purely arbitrary location that was designated the zero point. Similarly, in order to measure the relative vertical depth of measured fossils, an arbitrary point on the pole was chosen as depth zero, with the specimen depth defined as the height difference between the highest point of the specimen and this zero point. The actual location of any specimen was established with polar coordinates, specifically the distance and the direction of the specimen from the zero point pole, direction measured as number of degrees east of north. When a long bone was measured for a bearing (i.e., horizontal orientation), the vertex of the measured angle was arbitrarily defined as the end of the specimen with the highest elevation; as in the polar coordinate position, the angle of orientation was measured as the number of degrees east of north. Plunge (i.e., vertical orientation) was measured in degrees for all specimens for which a bearing was taken, the angle measured from the point of highest elevation to the lowest.

In taking these orientation data, not all specimens were considered equally important. Specimens recovered from spoil were neglected altogether, since their positional information had disappeared. Relatively small and/or unspectacular specimens (e.g., isolated Alligator teeth and coprolites) were also neglected. A full set of orientation measurements was taken for all long bones (i.e., any elongated bone that could have been disturbed by a current) whether identifiable or not, since these were the only elements for which a bearing and plunge could be meaningfully measured. The only exception to this procedure was the specimen DL 3, an Amebelodon rib, which was mistakenly removed without orientation measurements having been taken. Some elements with questionable ability to orient in a current such as mandibles and even a maxilla were also included in order to bolster the total sample size. Positional measurements, without bearing or plunge values, were taken for all specimens that were not long bones yet exceptional in some manner (e.g., skulls, associated vertebrae, and so on). A list of the specimens for which orientation measurements were taken is presented in Appendix 7, while the data are presented in Appendix 8. Figure 9-1 is a map showing the relative positions of all measured specimens collected during the 1991 field season.

State of Bone Preservation

The physical properties of fossilized bones can directly reflect the conditions associated with their preservation. The state of fossil bone preservation varies stratigraphically within Moss Acres Racetrack. The bones from unit 2 are uniformly poorly preserved, being fragile and at times distinctly crumbly. In some cases, the bone has been degraded almost to powder, probably by chemical leaching. The original shape of such bones is maintained only by the surrounding clay, a condition referred to by the informal descriptive term "pudding bone." In contrast, the bones in unit 3 tend to be much more solid than those in unit 2, though some isolated examples of pudding bone are known from this unit as well. One exceptional specimen that illustrates this stratigraphic variation in preservation is an *Amebelodon* skull with the field number DL 2. Encompassed by both units 2 and 3, that portion of the skull that lay within unit 3 is solid and well preserved, while the portion

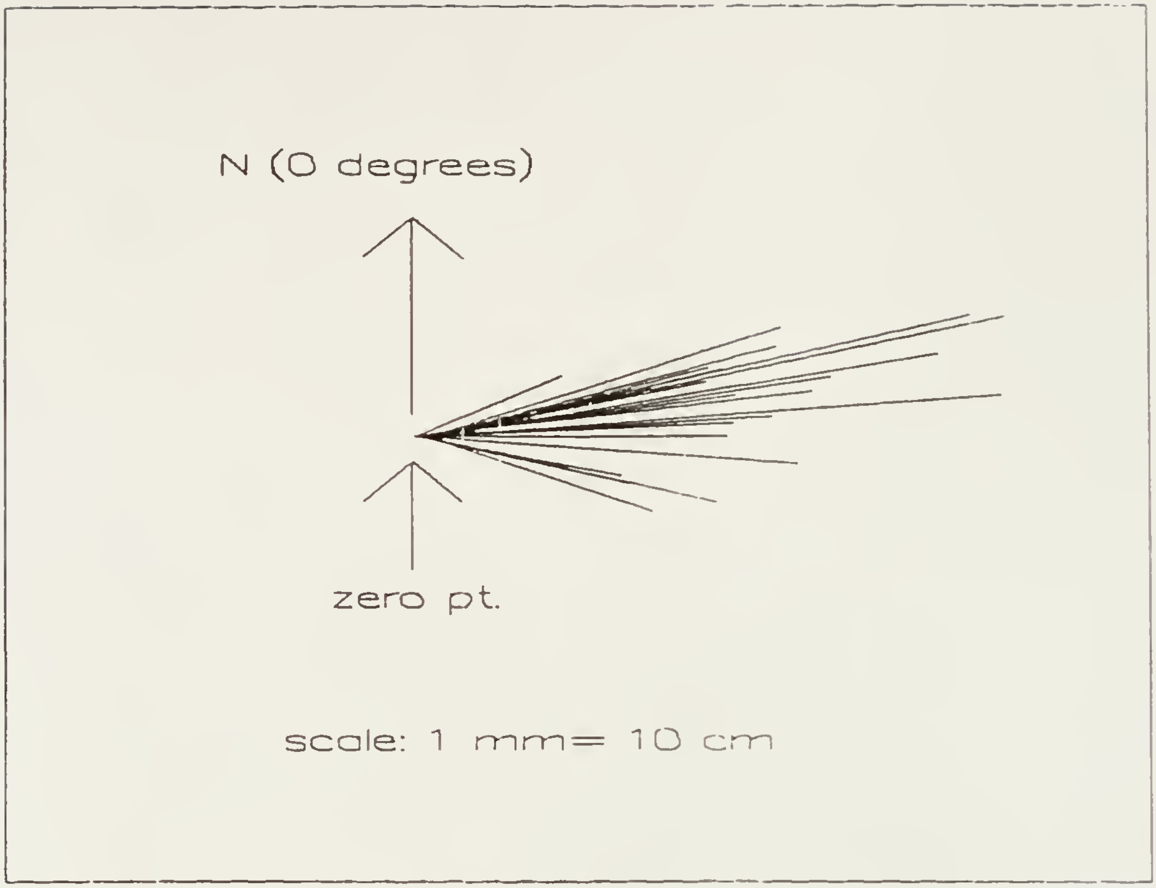

Figure 9-1. A map of the distribution of Moss Acres Racetrack specimens recovered during spring field season of 1991; the end of each line represents the distance and direction from the zero point for each specimen.

within unit 2 is very poorly preserved, much of it reduced to pudding bone.

Although the bones in unit 3 are for the most part very well preserved, the skulls are consistently crushed through compaction of the surrounding clay matrix. No specimens show signs of wear from water transport. Three increasingly severe levels of water wear can be diagnosed by the following conditions: 1) ends and processes of bones slightly rounded, and surface pitted by sand grains (minimal); 2) bone shows significant wear but is identifiable, with rounded articular surfaces and processes, cancellous bone exposed near articular surfaces (moderate); and 3) the bone is unidentifiable, with articular surfaces and processes completely abraded (severe) (Pratt, 1986).

Most of the specimens from unit 3 show no unusual preservational features. However a small number of specimens show a distinctive pattern of cortical bone removal, reflecting unusual preservational conditions relative to the other specimens. Specimens exhibiting such wear include: UF 104242, a camelid astragalus; UF 90541, a juvenile camelid distal metapodial; UF 135825, an Aphelops distal metapodial epiphysis; UF 135829 and UF 135830, Aphelops metapodial ends; UF 115554, a juvenile Aphelops vertebra; and UF 93460, an equid distal humerus. Each of these specimens has had most of its cortical bone worn away to expose the underlying cancellous bone, and with the exception of the camelid astragalus has been softened to a distinctly chalky and flaky consistency.

Subaerial weathering is the most likely explanation for the removal of the cortical bone suffered by these degraded specimens. Behrensmeyer (1978) described the manner in which bones decompose when exposed on the surface. The decorticized specimens correspond perfectly with the last stage in the decomposition process, in which the bone has been reduced to a mere core of cancellous bone (or a partial core, if as is common the bone was weathered unevenly). Bone decomposition is caused primarily by physical stress induced on the bone microstructure by rapid, continuous alternation in microclimatic conditions (particularly temperature and humidity). Other factors that can be important include bacterial activity and an alkaline, chemically corrosive soil. The rate of bone decomposition can vary with environment, microclimatic fluctuation being more severe in some environments than others. Because of the ameliorating effects of water, bones in aquatic or near aquatic environments experience a relatively slow rate of subaerial decomposition relative to arid or semiarid environments (Behrensmeyer, 1978). Thus the decorticized specimens were probably exposed to different, presumably drier conditions than the others. Conceivably they were transported only a few meters before being buried in the site. The geological evidence presented in chapter 2, the absence of water-worn bones, and bone orientation evidence (see below) all argue against a consistent significant current inflow into the site. Temporary flooding conditions, however, could have washed bones into the site (in this case probably only over a short distance, as evidenced by the absence of obvious water wear from these specimens). The relatively low density of the decorticized bones would have given them considerable buoyancy, and thus allowed them to be moved by even a minor current.

Three specimens in the Moss Acres Racetrack fauna show evidence of pre-burial gnawing. The *Amebelodon* mandibular tusk UF 97268 has two adjacent parallel grooves on its internal surface approximately 12 inches from its distal tip. The antilocaprid astragalus UF 116847 has a continuous series of well defined, closely spaced overlapping striations that extend radially along the entire margin of both its dorsal and ventral surfaces, resulting in a facet on both surfaces. And finally, the centrum of a juvenile rhino vertebra, UF 115554, has a single deep groove-like gouge on one side, with two distinct punctures on the side opposite from the gouge.

Bone gnawing is a typical carnivore activity (practiced by both predators and scavengers) that increases the amount of energy available from a carcass (Hill, 1980). However rodents such as modern *Hystrix* (the African porcupine) are also known to gnaw bones, though to obtain minerals rather than energy (Brain, 1980). The gnaw marks on the *Amebelodon* tusk and the antilocaprid astragalus more plausibly represent the result of rodent rather than carnivore gnawing for the following reasons: 1) the gnaw grooves are too closely spaced to have been created by a carnivore premolar or molar cusp; 2) the gnawed surfaces are concentrated on regions from which energy-rich tissue such as cartilage is largely or completely absent (the gnaw marks on the astragalus are concentrated away from the cartilaginous articulating surfaces, while the tusk lacks cartilage altogether); and 3) there are no signs of puncturing of the bone surface.

The aforementioned gnawing activities clearly occurred prior to burial of the bones. The antilocaparid astragalus in all likelihood was gnawed on land as part of a decomposing carcass and then subsequently washed into the site in a fashion like that proposed for the degraded specimens above. However, water transport would have surely visibly damaged if not destroyed the fragile _Amebelodon_ mandibular tusk. Therefore, this specimen was most likely gnawed while actually within the aquatic environment. This could have occurred if the _Amebelodon_ individual had died in (relative to its body size) shallow water, with at least this one tusk left exposed in the air within the carcass until burial (either by fluvial means or more likely, passive sinking into underlying sediment [see below]). The rodent or rodents could have reached the tusk by either swimming or else using aquatic vegetation as a bridge.

The deep gouge and associated puncture marks on the juvenile _Aphelops_ vertebra are most likely carnivore bite marks. Each puncture represents an anchorage site for one tooth that allowed an opposing tooth to gouge the bone. The gnawed vertebra shows signs of having been weathered. Thus, it must have experienced four taphonomic stages: carcass decay, exposure of bone, gnawing, subaerial weathering, and finally burial in unit 3.

Bone Association

Degree of fossil bone association (i.e., the tendency for bones from a single animal to either lie close together or be separated) provides important information regarding the conditions to which the bones were exposed both before and during burial. Such information is crucial to determining whether the fauna represents an *in situ* community, or a transported assemblage containing animals that lived in separate communities (Behrensmeyer et al., 1992). Appendices 1-6 list all of the catalogued vertebrate specimens recovered from Moss Acres Racetrack in the collection of the Florida Museum of Natural History, with the following exceptions: the *Enhydritherium* skeleton, UF 100000; the two known *Pliometanastes* specimens, UF 95400 (associated partial skeleton) and UF 69947 (isolated scaphoid); and the cranial specimens referred to *Amebelodon britti* in chapter 3. A survey of these specimen lists reveals that associated specimens are very common in the assemblage. Of the 350 cataloged specimens in the Moss Acres Racetrack fauna, 114 represent associations of two or more specimens, approximately a third of the total fauna, with 20 of these specimens representing partial or complete skeletons. Though exact figures of this kind are unavailable for other sites, this is clearly an extraordinarily high level of association.

The abundance of associated specimens at Moss Acres Racetrack says a great deal about the preservational conditions at the site. Carcasses that are subaerially exposed for long periods or transported a significant distance prior to burial are subjected to a number of strong disassociative factors, including scavenging, trampling, and hydrodynamic sorting (Voorhies, 1969; Hill, 1979; and Brain, 1980). The large number of associated specimens in the Moss Acres Racetrack fauna suggests that these dissociative factors were relatively unimportant in forming the fossil assemblage. Most Moss Acres Racetrack animals must have been buried soon after the death with little if any pre-burial transport. This finding is consistent with evidence provided by the preservational state of the majority of bones from the site (see above). Based on these two independent lines of evidence, there seems little doubt but that the majority of the animals in the assemblage died either within the immediate vicinity of or more likely directly within the aquatic environment in which they were preserved.

Beyond the abundance of associated skeletons, Moss Acres Racetrack is a particularly unusual site in preserving a large number of associated but isolated body parts, mostly entire limbs or limb segments (e.g., a foreleg or a manus) with no trace of the rest of the skeleton. Unlike the whole skeletons, which can easily be explained by the mechanism of swift post-mortem burial, the large number of these isolated limbs defies obvious explanation. Previous studies have found that scavenging activity is the primary means of terrestrial carcass disarticulation (e.g., Brain, 1980; Hill, 1979; and Hill, 1980), and as was mentioned above the vast majority of specimens at Moss Acres Racetrack experienced little or no pre-burial exposure to scavengers or other destructive terrestrial agents. Thus, these specimens must have been separated from their main caracasses within the aquatic environment of the site. However, normal aquatic dissasociation cannot account for this situation either. The skeletal disarticulation of unburied carcasses in aquatic conditions tends to begin at the distalmost regions (i.e., the phalanges) and procedes proximally (Hill, 1979; Hill, 1980), a process inconsistent with the formation of isolated associated limbs (though it may plausibly explain non-limb associations such as strings of vertebrae and the numerous isolated limb elements, particularly phalanges and metapodials) (Hill, 1979). Thus, it seems inescapable that these specimens were buried before significant dissociation of the carcass could occur.

The key to solving this puzzle seems to lie in understanding the burial process itself, since this ultimately determined which specimens were protected from destructive agents and which were not. The various modes of specimen burial can be divided into two major categories, ex *situ* and *in situ*. *Ex situ* or depositional burial is the active covering of a specimen by fluvially-deposited sediment from outside the site. *In situ* burial, in contrast, is passive subsidence of a specimen into already existing sediment. *Ex situ* burial processes do not plausibly explain this unusual preservational pattern for two reasons. First, *ex situ* burial may result in the preservation of isolated portions of a carcass only if one presupposes that isolated pockets within the sediment blanket had conditions suitable for fossil preservation (e.g., anoxic conditions, appropriate pH, and so on). However, such a haphazard process is unlikely to have targeted limbs over other portions of the carcass. Secondly, there is neither geological nor taphonomic evidence for continuous deposition of sediment into the site at a rate sufficient to bury and preserve large specimens (see chapter 2 and below), though the possibility of sporadic major deposition from flooding cannot be ruled out.

The most plausible scenario for *in situ* burial in this case has carcasses in the water (perhaps mired) sinking into the soft clayey substrate on the bottom under their own weight. The limbs, as the thinnest parts of the body, would have tended to sink more easily and deeply than the torso, and could have either sunk to a level within the clay where conditions were suitable for preservation separate from the rest of the carcass, or else possibly could have been the only portion of the body buried at all if the rest of the body resisted sinking. In another scenario involving in situ burial, the limbs were buried not under their own weight, but rather by the trampling of other animals (the softness of the substrate could have protected the trampled bones from the crushing they would surely have experienced on dry land; note that isolated elements could have been buried in this manner as well). Unlike the ex situ burial hypothesis, there are no obvious factual inconsistencies that conflict with either of the two in situ burial scenarios described above. Indeed, they are consistent with the presence of rodent gnaw marks on an *Amebelodon* mandibular tusk that in all likelihood had never been exposed on dry land.

While explaining the presence of isolated associated limbs, the in situ burial hypothesis does not easily explain the burial of the numerous isolated bones that constitute two-thirds of the fauna, though trampling may account for at least some of them. It therefore seems inescapable that some form of fluvial deposition and burial must have occurred at the site as well as in situ burial. Considering the absence of sand grains and other impurities in the sediment, the absence of water wear on the bones, the presence of peat, and the lack of any clear orientation in the long bones preserved in the site (see below), one must conclude that the fluvial burial was the result of either sporadic and rapid sedimentary deposition (e.g., from flooding), or else very slow, gradual deposition (e.g., a small and/or slow stream flowing into the site, or perhaps flowing ground water with a fine sediment load; see chapter 2). This conclusion is supported by the numerous isolated, untransported bones in the assemblage, which indicate that the carcasses lay unburied for considerable periods of time and gradually disintegrated piece by piece.

Bone Orientation

Long bones (e.g., ribs, various elongated limb bones, and the spinous processes of thoracic vertebrae if broken free) tend to respond to unidirectional currents by hydrodynamically aligning themselves along the path of least resistance. This hydrodynamic realignment can indicate both the presence and the direction of a current in the preserving environment, information important for understanding such preservational aspects of a fossil assemblage as mode of transport and burial of specimens.

The data for bearing and plunge of 27 Moss Acres Racetrack specimens are presented in Appendix 8. The sample size is very small for this type of analysis; for example Voorhies (1969) utilized orientation data from 450 specimens in a similar taphonomic study. Because of the small size of the data set, orientation data were taken from bones that would otherwise be considered of marginal usefulness at best, for example an equid maxilla (DL 9) and an associated/articulated equid hindlimb (DL 8) (the associated hindlimb is considered marginal because the specimen was presumably buried before the joint connections were completely severed, and a jointed specimen exposed to a current can be flexed along its length and thus have its "true" orientation distorted).

The bearing values presented in Appendix 8 are portrayed graphically by a rose diagram (essentially a histogram of bearing values in degrees in quadrant format, relative lengths of the lines indicating the number of points in that range) in Figure 9-2A. A rose diagram indicating a current bias in a population of specimens should show a distinct concentration of values in two supplementary directions, for example 0/180^0, 120/300^0, and so on. No such pattern is visible in Figure 9-2. However, the pattern does not resemble a simple random distribution; the large majority of the values lie on a single half of the plane separated by a 135-315^0 dividing line. Another method of graphically portraying orientation data to determine the likelihood of a current flow is a stereonet projection as shown in Figure 9-2B, in which orientation data are displayed as a radial scatterplot of points; the angular component of each point represents its bearing, and the distance of the point from the center represents the plunge of that specimen in degrees. In a stereonet projection, a significant current is indicated by a tendency for the points to form a rough line between supplementary regions through the zero point, the direction of this line being the direction of current flow (Voorhies, 1969). As in Figure 9-2A, the points are heavily loaded to one side of the plane (not surprising considering that both

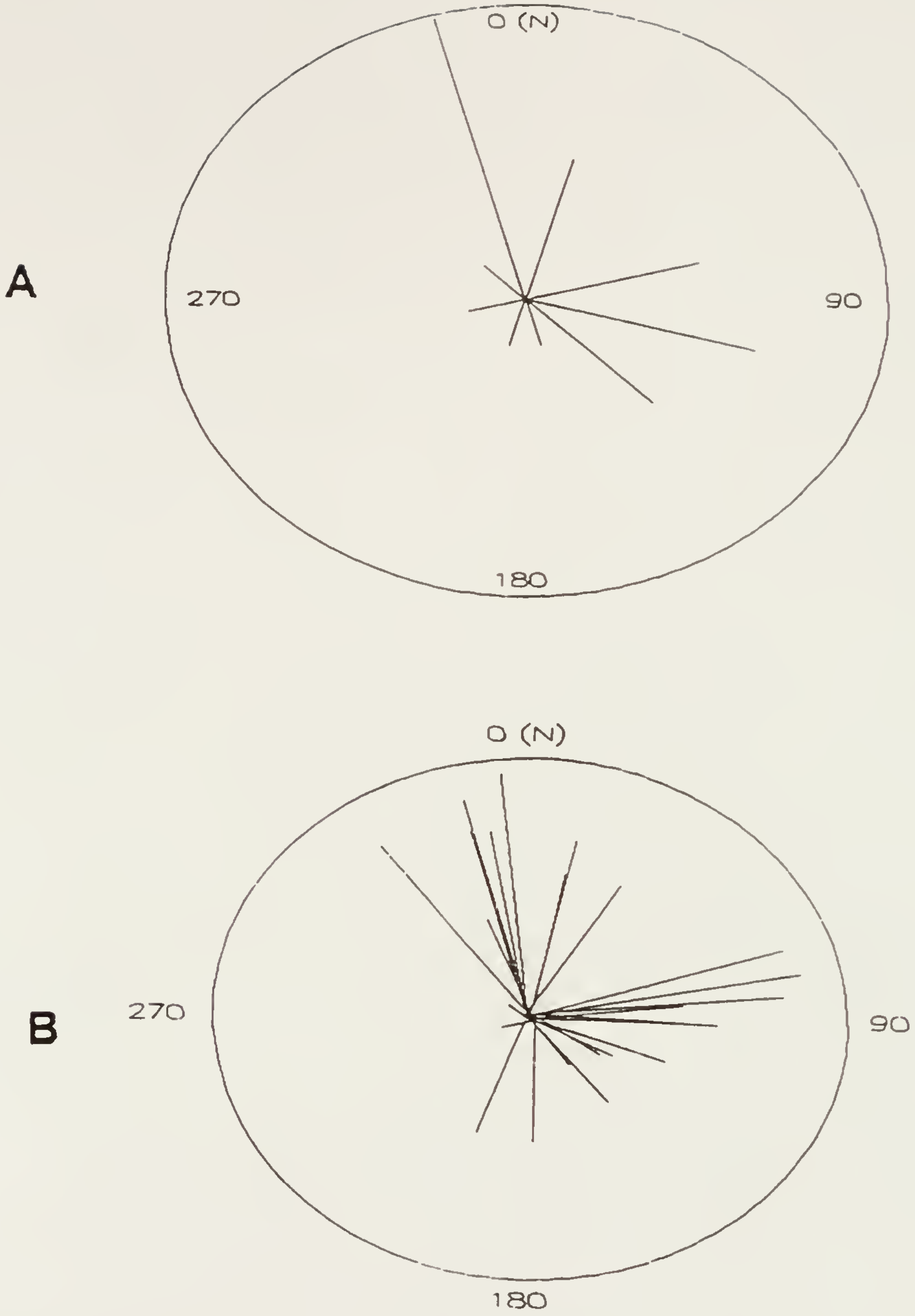

Figure 9-2. Diagrams portraying Moss Acres Racetrack bone orientation data as presented in Appendix 7. A) rose diagram, the number of specimens in each degree range indicated by line length; B) stereonet projection, line length representing specimen plunge.

graphs utilize the same bearing values), but the plunge values appear to be random. Thus, there is no specific evidence for a current having passed through the Moss Acres Racetrack. This negative evidence is hardly conclusive however, considering the small size of the data set. In addition, there is no ready explanation for the asymmetrical distribution of the bearing values beyond random chance.

Faunal Biases

Taphonomy is sometimes defined as the study of biases in the preservation of fossil faunas (e.g., Raup and Stanley [1978]). Based on the above taphonomic analysis, we can now examine possible preservational biases and how they may have distorted our view of the original paleofauna that existed at the Moss Acres Racetrack site.

One of the most important sources of faunal bias in fossil assemblages is transport into the preservational site (Voorhies, 1969). Mode of transport influences the potential of individual specimens to be preserved (e.g., through specimen durability and sorting effects), and the locality(ies) from which these specimens may originate. As discussed above, the evidence indicates that the vast majority of specimens preserved at Moss Acres Racetrack site were not subjected to significant transport or subaerial weathering, the animals in most instances probably having died directly within the site. Thus, neither specimen durability nor potential for fluvial sorting should have greatly influenced the fossil fauna observed at Moss Acres Racetrack.

Another factor that may introduce bias into the preserved assemblage is habitat preference. If animal remains are not transported into a site, then the only animals that will be preserved in significant numbers are those that actually die in the preservational environment itself, in this case an apparently permanent body of water. Thus, the resulting fossil fauna should be biased in favor of animals that either lived in an aquatic environment permanently or else spent a significant amount of time in both aquatic and terrestrial environments. The abundant Alligator and aquatic turtle material, as well as the sporadic gar and the singular duck and Enhydritherium specimens certainly belong to the first category. Amebelodon evidently belonged to the second category, having fed in both terrestrial and aquatic habitats (see Lambert, 1989; 1992). However the majority of the fauna is composed of cursorial ungulates (specifically the varied equids and rhinoceros Aphelops), animals that are clearly highly terrestrial. Thus, the Moss Acres Racetrack fauna is biased in a surprising manner. However, this bias in favor of terrestrial mammals may be explained to some degree by a scenario in which numerous animals waded into the water to drink or perhaps bathe (particularly Amebelodon) and then subsequently died, perhaps due to becoming mired. Another possible scenario, complementary to that mentioned above, is that some of the smaller ungulates were dragged into the water during alligator predation.

Other surprising biases exist in the Moss Acres Racetrack fauna as well. For example, though the environment was aquatic, small aquatic vertebrates (e.g., fish, amphibians, and water snakes) are a miniscule part of the fauna. Only seven unreworked fossils in this category have been recovered from Moss Acres Racetrack, all belonging to bony fish. This rarity cannot simply be attributed to a failure to specifically search for microvertebrate remains, since a considerable quantity of Moss Acres Racetrack matrix was screened for microvertebrates without success (there is no record of the exact amount of substrate that was processed) (Poyer, pers. comm.). Micromammal remains are also completely absent from the Moss Acres Racetrack site despite direct evidence for their presence in the original fauna in the form of trace fossils (e.g., rodent-gnawed specimens). Surprisingly, terrestrial carnivores are virtually absent from the fauna despite the abundance of herbivores. This bias may have its basis in either specimen sample size or real ecological factors (see chapter 10).

The rarity of small aquatic vertebrate fossils from the Moss Acres Racetrack fauna is almost certainly the result of a taphonomic rather than an ecological bias. The abundance of emydid turtles and alligators in the fauna indicates that a thriving aquatic community was present, and small aquatic vertebrates would certainly have been part of such a community. Moreover this bias, whatever its nature, is not characteristic of all preservational environments broadly similar to that of Moss Acres Racetrack. For example amphibians and fish are abundant at the Withlacoochee River 4A site, which had preservational conditions very similar to those of Moss Acres Racetrack (i.e., a sinkhole filled under extremely low energy conditions by apparent Alachua clays), including numerous highly compressed fish skeletons within clay lamina reminiscent of specimens from the Eocene Green River Formation. Possibly the bias is based on size, large fossils being favored by some taphonomic process over small fossils such as those of small aquatic vertebrates. Smith et al. (1988) noted a tendency for fish, small fish in particular, to be poorly represented in flood plain facies, explaining their absence on the basis of their vulnerability to biological and mechanical destruction. Conceivably the difference between the Moss Acres Racetrack and Withlacoochee River 4A sites lies in a greater sedimentation rate in the Withlacoochee River 4A, small vertebrates having been buried before they could be destroyed.

In the case of the absence of micromammal fossils, again we have a situation where large animals are preserved in preference to small animals. Unlike the small aquatic vertebrates, one could potentially attribute the absence of micromammal fossils at Moss Acres Racetrack to the fact that, with possible rare exceptions (e.g., analogs to the modern star-nosed mole [Condylura cristata], and the muskrat [Ondatra zibethicus]), they did not live directly within the preservational environment and were too small to become mired like large terrestrial animals. However despite the fact that it appears preservationally similar to Moss Acres Racetrack, micromammals (specifically rodents and leporids) are reasonably common in the Withlacoochee River 4A fauna (Becker, 1985; pers. observ.). Again, this difference may be based on different sedimentation rates between the two sites.

Carnivore fauna differences may also help explain the microfaunal differences between Moss Acres Racetrack and the Withlacoochee River 4A, assuming that the bias against carnivores in the Moss Acres Racetrack fauna reflects ecological reality. Carnivores can strongly influence the preservation of microfaunal remains. Mellet (1974) observed that microvertebrate remains are commonly concentrated in sites through the accumulation of carnivore scats (he coined the term coprocoenosis to describe this phenomenon). Similarly in a study of modern bone preservation in savannas, Behrensmeyer and Boaz (1980) found micromammal bone remains primarily in areas were carnivore scat was abundant. Pratt (1986) attributed the abundance of micromammal specimens at the Thomas Farm site partly to the feeding activities of terrestrial carnivores, including birds (e.g., owls) and small to medium sized mammalian carnivores. The Withlacoochee River 4A fauna is known to have had carnivores of a size suitable for preying on micromammals, including

Osteoborus orc (relatively abundant), a probable fox (?*Vulpes*) and a hawk (*Buteo* sp.) (Becker, 1985; Webb, 1969), whereas as noted above terrestrial carnivores are extremely rare in the Moss Acres Racetrack fauna. Thus it is conceivable that a real ecological bias in the Moss Acres Racetrack fauna, namely the scarcity of small to medium-sized carnivores, helped create a taphonomic bias against the terrestrial microfauna. It should be noted however that the evidence supporting this hypothesis is clearly circumstantial in nature rather than direct, a common problem in paleoecological analysis.

It is worthwhile to end this discussion of the taphonomy of the Moss Acres Racetrack site by emphasizing the role that chance played in determining what taxa are known for the fauna via the process of field collection. Many of the taxa in the Moss Acres Racetrack fauna are known on the basis of single, sometimes poorly preserved specimens (e.g., the *Apalone* partial carapace and plastron, the anatid partial coracoid, the cf. *Aepycamelus* cervical vertebrae, the antilocraprid astragalus, the "*Pseudoceras*" partial tibia, the tayassuid partial milk premolar, and the *Enhydritherium* partial skeleton). Even a mild shift of fortune, for example a machine blade cutting just a few inches deeper during the original excavation of the site, could have eliminated knowledge of any of these taxa in the fauna. By the same token, a mild shift in fortune could have conceivably brought to light taxa in the fauna currently unknown, for example additional terrestrial carnivores, the mylodontid ground sloth *Thinobadistes*, a mylagaulid rodent, or the proboscideans *Gomphotherium* or *Mammut*. Rare taxa tend to produce such distortions in almost all fossil assemblages, with the problem being minimized only by thorough locality excavation in order to maximize sample size.

CHAPTER 10

THE PALEOCLIMATE AND PALEOECOLOGY OF THE MOSS ACRES RACETRACK SITE

The ecology of any site can be broadly defined as the the sum total of the interactions between organisms and their environment, both biotic and abiotic. The faunal component of the Moss Acres Racetrack site has already been discussed, and much of the abiotic component of the environment was discussed in previous chapters on the geology and taphonomy of the site. This chapter will focus on the climate, flora, and community relations within and between the flora and fauna of the site.

Paleoclimate

The modern climate of north Florida, which encompasses the Moss Acres Racetrack site, is referred to as humid subtropical in the Koppen climatic classification system (sometimes informally called warm temperate). In this system, a humid subtropical climate is characterized by: 1) a coolest month with an average temperature between 18° and -3° C; and 2) a warmest month with an average temperature above 22° C. The yearly distribution of precipitation can vary considerably in humid subtropical climates, depending in part on the relative influence of such factors as polar cyclones and moist tropical air. Extremely dry months are uncommon however, precipitation being much more evenly distributed through the year than is normal for arid and semiarid climates. Yearly precipitation levels typically range from 750-1500 millimeters. Latitudinally modern north Florida lies near the southern boundary of the humid subtropics, a savanna climate extending as far north as the Everglades in South Florida (Critchfield, 1983).

Over most of the Cenozoic beginning in the Eocene, the climatic trend in North America has been towards a progressive cooling and an increase in the seasonality of precipitation, culminating in great glacial advances and semiarid grasslands that coexisted periodically throughout the Plio-Pleistocene (Webb, 1977; 1984; and 1989). Extrapolating this trend backwards in time, one would predict that north Florida had on average a warmer and wetter climate during the Hemphillian than the present. Despite the aforementioned climatic trend however, it is not necessarily the case that precipitation in north Florida during the Hemphillian was less seasonal or the temperatures warmer than today, since these aspects are influenced in a complex manner by a variety of interactive regional factors including high pressure cells, ocean currents, jet streams, temperature, and longitudinal/latitudinal geography (Critchfield, 1983; Battan, 1979).

North America, including Florida, is commonly considered to have been dominated by savanna during the Miocene (e.g., Webb, 1977; 1984; 1989; Leite, 1990; and Hulbert, 1982). In this case the term savanna does not refer to a climate but rather a specific landscape, defined as open country dominated by herbaceous plants such as grass, with trees present but scattered so that a consistent canopy is absent (e.g., Webb, 1977; Sarmiento, 1984). In the Koppen climate classification system, however, a savanna is defined as a tropical climate (i.e., coolest average monthly temperature 18° C or higher) with highly seasonal rainfall so that the total precipitation in the driest month is less than 100 millimeters-r/25, where r equals the average annual precipitation in millimeters. A landscape such as that described above is considered typical of savanna climates, but is not a prerequisite for them. Another type of climate that is characterized by distinct rainfall seasonality and thus could in principle create a savanna landscape is the monsoon, here defined in the traditional sense as a seasonal alternation between a strong flow of moisture-laden air from an ocean onto land (the "wet" monsoon) and dry continental air towards the ocean (the "dry" monsoon). A weak monsoon effect is responsible for the short period of intense summer rainfall experienced by deserts of the American Southwest, as well as much of the summer rain on the Florida peninsula (Battan, 1979; Critchfield, 1983).

The available evidence indicates that, at least during the first half of the Hemphillian and probably the back into the late Clarendonian and Barstovian, north Florida was dominated by a savanna landscape (see below). The presence of a savanna landscape alone, however, does not allow one to draw ready conclusions about such regional climatic factors as temperature and rainfall. Other factors that can generate modern savanna landscapes include fire, physiographic flatness, and animal activity, with cattle grazing having been observed to create artificial savannas in regions of South America that would otherwise have been forest (Retallack, 1982; Sarmiento, 1984).

From the Barstovian to the early Hemphillian savanna landscapes dominated the Great Plains as well as northern Florida, extending as far north as 40° latitude (Webb, 1977; Hulbert, 1993a). However, it is not clear that this landscape was associated with a savanna climate. Modern savanna climates are driven by seasonal strengthening and weakening of tropical lows, mostly associated with the Intertropical Convergence Zone except near the poleward and equatorward boundaries of the climatic zone (Critchfield, 1983). Therefore it is extremely unlikely that the modern mechanism could have created a savanna climate so far north and so deep in the continental interior, even if temperatures were significantly warmer in this region (currently precipitation in the Great Plains is governed mainly by polar cyclones, with tropical influence very small). Indeed, there is evidence that the Intertropical Convergence Zone was weaker and/or considerably farther south than that of the present during the late Miocene (see below). A monsoon effect cannot easily provide a climatic explanation for these savannas either. For a monsoon effect to have significantly influenced the interior of North America during the late Miocene, out of necessity this region would have had to have been subject to intense summer heating (thus generating strong low pressure cells) to draw moisture from an adjacent warm body of water, most likely the Gulf of Mexico. However, paleobotanical climatic evidence indicates that summers were relatively cool in the interior of North America during the late Miocene (Wolfe, 1978; Hulbert, 1993a; see discussion below), so that a significant monsoon effect in this region is extremely unlikely.

It is unclear whether these late Miocene North American savannas were the result of climatic factors, non-climatic factors, or a combination of the two. However, indirect clues in combination with the floral landscape may help clarify the role of the climate. Because of the severe aridity of the dry season in a savanna (and monsoon) climate, typical modern savanna floras (particularly the grasses and other open country herbaceous plants) have alternating periods of activity, with the wet season characterized by high activity and subsequent high productivity and the dry season by low activity and and little or no productivity (Sarmiento, 1984; Bourliere and Hadley, 1970). Modern large herbivores, particularly grazers, commonly but not universally respond to these changing vegetational conditions through seasonal migration. During the dry season they seek regions with permanent water sources and thus continuously active vegetation, and then move away from these water sources during the wet season (Bourliere and Hadley, 1970; numerous papers in Sinclair and Norton-Griffiths, 1979; Owen-Smith, 1988). Thus, evidence of seasonal migration by herbivores, particularly grazers, living in a savanna landscape would provide circumstantial evidence for regional seasonal aridity at a locality, though there would still be ambiguity as to the temperatures experienced. (It should be noted that other factors could conceivably cause seasonal alternation in grass productivity, such as prolonged cold temperatures.)

Hulbert (1982) studied the population dynamics of the presumed grazing hipparionine equid Neohipparion at the Love site, a latest Clarendonian locality in north Florida with a distinct savanna fauna (i.e., a fauna with a mixture of grazers and browsers; see below). Based on evidence for discrete age classes in premolar wear, Hulbert concluded that these animals died seasonally at the site rather than continuously, and therefore that Neohipparion must have migrated to and from the site. Seasonal movement by a grazing animal such as Neohipparion within a savanna landscape is most plausibly explained by a savanna or monsoon pattern of rainfall, with regular, predictable dry seasons and corresponding grass inactivity away from permanent water sources. The Love site is distinctly older than Moss Acres Racetrack by approximately 1 1/2 million years. However, the savanna that existed in north Florida during the Love and Moss Acres Racetrack time was part of a continuum that had dominated North America and Florida in particular since the Barstovian (Webb, 1977), and there is no evidence to indicate that the climatic conditions that created the Clarendonian savannas were different from those that created the early Hemphillian savannas or those of the Barstovian. There are however climatological reasons to question whether the climatic conditions that generated the Florida savannas were identical to those that generated the interior savannas of the Great Plains (see above).

Oxygen isotope data indicate that the global temperature was significantly warmer than the present during the early Hemphillian, probably due in part to minimal or nonexistent glaciation in North America and a less extensive glaciation of Antarctica than today (Webb, 1984; 1989). Faunal evidence supports this supposition as well. For example, during the late Miocene alligators and giant tortoises were present in the Great Plains as far north as Nebraska (Schultz, 1977; Skinner and Johnson, 1984), indicating that the continent experienced relatively mild winters. Palynological data, however, appear to contradict this picture. Palynofloras (including the palynoflora of Moss Acres Racetrack; see below) indicate that the late Miocene flora of southeastern North America had a strongly modern aspect. Deciduous trees were common and tropical plants largely absent, suggesting that the region experienced temperatures very much like those found in the region today (Graham, 1964; Webb, 1977). Indeed humid subtropical floras evidently extended much farther south during the late Miocene than today. For example, deciduous taxa such as oaks are abundant and tropical plants scarce in the late Miocene Veracruz palynoflora of southern Mexico (in modern times, this region lies in a pocket of rainy tropics within a savanna belt that is heavily influenced by the Intertropical Convergence Zone [Webb, 1977; Critchfield, 1983]). Wolfe (1978) obverved these same unusual latitudinal patterns in the floral macrofossil record of North America. Using leaf morphology as a climatic assay, he determined that the southern region of the continent was characterized by a distinctly temperate climate, with relatively cool winters (as cool or cooler than that found in the region today) and warm to hot summers, while the more northern regions tended to be more equable, with winters warmer than found in the region today and summers as cool or cooler. Dowsett et al. (1992) found evidence for a similar climatic pattern in North America during the Pliocene, reinforcing Wolfe's findings.

This proposed climate for the late Miocene of North America strongly contrasts the modern climate. The causal factors that could underlie this hypothetical climate are uncertain. Wolfe (1978) advocated a scenario invoking changes in the Earth's rotational inclination, with a subsequent redistribution of global insolation and thus a change in atmospheric and perhaps oceanic circulation.

Dowsett et al. (1992) speculated that the latitudinal transfer of heat through the oceans was greater during the late Miocene and Pliocene than today, though they did not offer a specific mechanism to explain this effect. Explanations aside, however, this proposed climate is consistent with the enigmatic circumstance of the synchronous presence of a distinctly subtropical (as opposed to tropical) flora as far south as southern Mexico and cold-intolerant animals like the giant tortoise in the northern Great Plains during the late Miocene.

Flora

Plant macrofossils are unknown from Moss Acres Racetrack. However, as was stated before isolated pockets of peat are found in unit 3 of the locality, and peat may contain identifiable plant microfossils, particularly pollen. To test this possibility, samples of peat-rich Moss Acres Racetrack clay were taken from previously unexposed sediment (to minimize the risk of contamination with modern pollen) and submitted to palynologist Dr. Barbara Hansen of the University of Minnesota for anlysis. Dr. Hansen examined two slides of sediment under a light microscope, and her findings are presented in Table
10-1.

Before discussing the significance of the Moss Acres Racetrack microflora/palynoflora, a brief discussion of the taphonomy of fossil pollen is in order. Pollen in modern

Table 10-1. Palynoflora and microflora of the Moss Acres Racetrack (common names and modern geographical ranges taken from Harrar and Harrar [1962], Peterson and McKenny [1968], and Zomlefer [1986])

Taxon	% or abundance	Common Name	Modern Geographical Range
(arboreal)			
Pinus	23	pines	N. Hemisphere
Juniperus type	1	redcedars	E. N. America
cf. *Tsuga*	1	hemlock	temperate Asia and N. America
conifer indet.	1		
Quercus	21	oaks	worldwide
quercoid	3		
Myrtaceae	3	myrtles	worldwide tropics
Ulmaceae	4	elms	worldwide
cf. *Planera*	1	waterelm	SE. N. America
Ulmus	1	elms *s.s.*	N. Hemisphere
Nyssa	1	blackgums	E. N. America
Myrica type	1	bayberry	worldwide temperate
cf. *Liriodendron*	1	tuliptree	E. N. America
broken periporate cf. *Juglans*?	1	walnut	worldwide
Acer negundo	1	boxelder	E. N. America
(nonarboreal)			
Poaceae	19	grass	worldwide
Tubuliflorae	4		
Artemisia	1	wormwoods & mugworts	N. America
Cyperaceae	1	sedges	worldwide
Rumex, broken?	1	docks	N. America
cf. *Ambrosia*	1	ragweed	N. America
Chenopodiacae/ Compositae	1	goosefoots, dandelions and cousins	worldwide

Table 10-1--continued

tricolpate, degraded	1	
Ficus-like spore	1 specimen	
sedge or grass epidermal cells		4 pieces
herb stomate	1 specimen	
small echinate pollen or spores	3	
triad/tetrad fungal spores	25	
degraded pollen		5
other indet.	3	
unknown pollen	14	

seed plants is dispersed primarily by two agents, wind and animal vectors (Weier et al., 1974). Of these, only wind is likely to have been a sigificant agent in transporting pollen into the site. Pollen grains are very small structures, and can be born by wind long distances under some circumstances, though they commonly are transported only hundreds of feet (Weier, 1974; Behrensmeyer et al., 1992). Thus, the palynoflora present in Moss Acres Racetrack will reflect not only the plants in the immediate vicinity of the site, but to an unknown extent those of the entire region.

The three most abundant identifiable taxa in the Moss Acres Racetrack palynoflora are the ubiquitous pines, oaks, and grasses. Grasses and oaks tend to be over-represented in palynofloras (Hansen, pers. comm.). Thus the abundance of the grasses is especially significant, strongly suggesting that much of the region was grassland. Trees are also a major part of the flora, with myrtles and elms common as well as pines and oaks. Thus, with grass abundant and trees well represented in the region, it is almost inescapable that north Florida had a savanna landscape during the late early Hemphillian just as it presumably did during the late Clarendonian. However, the actual structure of this savanna is unclear from this data; for example, it is uncertain whether trees were sparsely but uniformly distributed throughout the region to form a giant open, grassy woodland, or whether the trees were restricted to distinct pockets in the midst of open grassland. Hansen (pers. comm.)

hypothesized that this pollen assemblage suggests a grassland with scattered mesic forest, a characterization that does not preclude either of these potential savanna structures.

The Moss Acres Racetrack palynoflora strongly resembles a modern temperate flora of North America, particularly the eastern region of the continent. Only the Myrtaceae give this flora a distinctly subtropical aspect (Moss Acres Racetrack is latitudinally close to the modern northernmost boundary of the Myrtaceae in Florida [Zomlefer, pers. comm.]). The predominance of temperate taxa in the palynoflora implies that during the late early Hemphillian north Florida was subject to winter temperatures similar to or perhaps somewhat cooler than those experienced by the region today, a finding consistent with those of Wolfe (1978), Graham (1964), and Dowsett et al. (1992) described above.

As mentioned above, a distinct limitation on the usefulness of palynological data in paleoecological reconstruction is that the sample may cover a wide area, with the result that disparate plant communities may be combined into a single sample. Thus, an independent test of this data is desirable. The feeding guild structure of an herbivore community (referring to the broad feeding categories of grazing, browsing, and mixed feeding) can also provide information about the structure of the local plant community (i.e., forest versus savanna versus grassland) if little or no post-mortem transport has taken place (Shotwell, 1963;

Webb, 1983b), and thus may be used to check the reliability of palynological data.

Before one can examine the feeding guild structure of a given community, it is necessary to first assign the taxa present to their appropriate guilds. The feeding guilds of extinct ungulates have been assessed on a number of different bases, with relative hypsodonty being one of the most commonly used (i.e., hypsodont teeth equals grazer, brachyodont teeth equals browser) (Shotwell, 1963; Webb, 1977; MacFadden, 1992). However, Webb (1983b) used a scatterplot of estimated body weight versus molar volume to determine the guild categories of a number of Miocene ungulates. A list of the herbivore taxa known from Moss Acres Racetrack and their guild assignments are presented in Table 10-2. Many of the assignments are based on the findings of Webb (1983b). Those equids not examined by Webb (1983B) appear to be plausible grazers based on their overall similarity in molar structure to those taxa found to be grazers by Webb, all being both moderately to very hypsodont and lophodont. However, Hulbert (1993a) pointed out that degree of hypsodonty reflects the amount of abrasive material consumed while feeding rather than the strict amount of grass consumed (for example, Antilocapra is a mixed-feeder despite being very hypsodont), and thus is not a reliable indicator of diet (presumably this reasoning could be used to disqualify molar volume as a dietary indicator as well). Nevertheless MacFadden (1992) considered all of these equid

Table 10-2. Feeding guild categories of Moss Acres Racetrack herbivores.

Taxon	Feeding Guild Category
Xenarthra	
Megalonychidae	
Pliometanastes protistus	Browser
Proboscidea	
Amebelodon britti	Browser (see chapter 3)
Perissodactyla	
Rhinoceratidae	
Aphelops mutilis	Grazer (see chapter 7)
Equidae	
Hipparion cf. *tehonense*	Grazer[1]
Neohipparion eurystyle	Grazer[1]
Calippus mccartyi	Grazer[1]
Cormohipparion emslei	Grazer
Cormohipparion plicatile	Grazer
Nannippus aztecus	Grazer[1]
Nannippus morgani	Grazer[1]
Dinohippus sp.	Grazer[1]
cf. *Astrohippus*	Grazer
Artiodactyla	
Tayassuidae	Mixed[1]
Camelidae	
Aepycamelus or *Megatylopus*	Browser or Mixed[1]
Hemiauchenia sp.	Mixed[1]
Gelocidae	
new genus near *Pseudoceras*	Browser
Dromomerycidae	
Pediomeryx hemphillensis	Browser (see chapter 6)
Antilocapridae	
genus indeterminate	Indeterminate

1: guild category taken from Webb (1983b) genera to be grazers on the basis of different evidence, their muzzle and incisor morphologies (see below). The ground sloth Pliometanastes is assigned to the browsing guild on the basis of the strong adaptive trend within this group in both extinct and extant forms (Simpson, 1980; Webb, 1978). The new genus and species near Pseudoceras (henceforth to be referred to as "Pseudoceras") is assigned to the browsing guild because of its strong morphological and probable ecological similarity to such small browsers as the small South American deer Mazama and African duikers (Cephalophus) (Nowak and Paradiso, 1983; Becker, 1985). The unidentified antilocaprid is not assigned to a guild because of apparent variation within the family; the modern antilocaprid Antilocapra is an opportunistic mixed feeder (Nowak and Paradiso, 1983; Whitaker, 1980), while Webb (1983B) found the antilocaprid Merycodus to be a grazer (this may be an example of the effect cited by Hulbert [1993a] above).

A savanna fauna is a fauna that, carnivores aside, contains a mixture of both browsing and grazing herbivores (with grazers dominant, but browsers always present in significant numbers), in contrast to a forest fauna that is heavily dominated by browsers and an open grassland (steppe) fauna that almost exclusively contains grazers (Webb, 1983b). A survey of the data in Table 10-2 shows that of the 17 large herbivore taxa known from Moss Acres Racetrack and assigned to guilds, ten are grazers and seven either browsers or mixed feeders, surely a sufficiently balanced mixture to justify calling the Moss Acres Racetrack Local Fauna a savanna community. However, as is common in savanna communities, this taxonomic balance is not reflected in the number of individual animals belonging to the different guilds. There are far more grazing individuals than browsers in the recovered fauna, with the rhinoceros Aphelops and the equids as a group constituting the vast majority (see Appendices 3 and 6). (Note however that the feeding guild assignment of Aphelops is somewhat tentative; see chapter 7.) In contrast, of the browers and mixed feeders only Amebelodon is reasonably common (see Chapter 3), with the other taxa being quite rare (Pediomeryx is represented by a minimum of three individuals, Pliometanastes by two individuals, and the other browsing/mixed-feeding taxa by only a single individual each).

As with the palynological data, the feeding guild structure of the Moss Acres Racetrack herbivore fauna says nothing definitive about the vegetation in the immediate vicinity of the site. One could argue that the great abundance of grazers in the fauna indicates a local predominance of grassland. However, grazers may be locally abundant in forests and woodlands under some circumstances. For example, the grazers Equus and Bison are the most common herbivores in the late Pleistocene Rancho Labrea Local Fauna, despite the fact that plant macrofossils show this area to have been significantly forested (indeed, there is direct evidence that these grazers were feeding on dicotyledonous leaves rather than grass) (Akersten et al., 1988; Warter, 1976; Kurten and Anderson, 1980). Grazers are also known to concentrate heavily in woodlands in the Serengeti of modern Africa, which they use as a dry season refuge (Maddock, 1979; see below). Similarly, the presence of browsers does not guarantee that trees were concentrated in the immediate vicinity of the site. As a permanent source of fresh water, Moss Acres Racetrack could have drawn browsers a significant distance away from wooded areas for drinking and bathing if water became scarce during dry seasons (though such dry seasons would have enhanced the tendency for woodland to have been present around the water source; see below).

In the case of Moss Acres Racetrack, abiotic ecological factors are probably a more reliable indicator of the nature of the local plant community than the fauna or pollen. Modern African savannas do not consist of simple homogeneous stretches of grassland with scattered trees. Rather they are distinctly patchy in their structure, with some areas being virtually treeless open grassland and others having a concentration of trees great enough to justify calling them woodland. A number of different ecological factors create this mosaic within the savanna, including soil types, fire activity, and the activity of large herbivores. However, one of the most powerful influences on the distribution of trees in modern savannas is the availability of permanent water, with trees concentrating and even forming forests around such permanent water sources as rivers and lakes (Sinclair, 1979a;

Owen-Smith, 1988). It should be noted that this pattern is a tendency and not a strict rule; for example, some African savanna river shorelines and floodplains are lined with extremely tall, dense grass such as papyrus (Smithers, 1983). Moss Acres Racetrack was a permanently filled pond/marsh in the midst of what evidence strongly indicates was a savanna. Thus if modern African savannas are assumed to be a proper ecological analog (particularly in terms of rainfall pattern), one would expect the area immediately around Moss Acres Racetrack to have been distinctly wooded, though possibly with dense tall grass covering its immediate shoreline (see below).

The presence of peat in Moss Acres Racetrack is direct evidence that plants lived within the aquatic environment. Unfortunately, none of the material in the examined peat beyond the pollen was sufficiently preserved to be identified. Some of the taxa in the palynoflora however are commonly or strongly associated with aquatic environments, namely the Cyperaceae, _Rumex_, _Planera_, _Acer negundo_, and _Nyssa_ (Zomlefer, 1986; Harrar and Harrar, 1962; Peterson and McKenny, 1968), and it is plausible that these taxa were present near the shoreline of the site. Other plausible but unobserved taxa that could have lived directly in the aquatic environment include an assortment of algae, cat-tails (_Typha_), pondweeds (_Potamogeton_), duckweeds (_Lemna_), pickerelweeds (Pontederia), and water-lillies (Nymphaea), all of which are common in modern north Florida (Zomlefer, 1986).

Fauna

The paleoecology of the Moss Acres Racetrack fauna can be examined from two different aspects: 1) the ecological basis for the formation of a community with this particular structure at this locality, and 2) intracommunity interactions. There is considerable overlap between these two aspects, so to an extent this division is arbitrary. Nevertheless this is one practical way to approach to this subject.

The fundamental factor that led to the formation of the aquatic community at this site is obvious, namely the presence of permanent water and its attendant food sources. The emydid turtle Pseudemys is environmentally indicative of the local water conditions, modern members of this genus requiring relatively clear water, a good supply of aquatic vegetation, and a soft bottom (the latter two conditions have already been implicated by other lines of evidence). The diet of modern Pseudemys is omnivorous, but the major portion consists of algae and duckweeds (Dundee and Douglas, 1989). Modern Apalone is primarily a predator on small vertebrates and arthropods (Anderson, 1965), and its presence supports the speculation made in the previous chapter that a small aquatic vertebrate fauna must have been present at the site despite the absence of direct fossil evidence. The gar

Lepisosteus probably fed on the same type of prey as Apalone. The presence of Alligator provides little insight into the overall ecology of the site. Modern Alligator is tolerant of a wide variety of aquatic conditions (and indeed at times may act to maintain aquatic conditions during dry spells by expanding watering holes) and is a highly oporturistic feeder, though the by far the largest part of its diet beyond the juvenile stage consists of small to medium sized aquatic vertebrates (e.g., turtles, fish, snakes, and water birds like ducks and herons). However, modern alligators may occasionally prey on medium to large sized terrestrial mammals (e.g., dogs and cattle) (Dundee and Rossman, 1989), and most likely alligators preyed on many of the mammals that frequented the site, particularly relatively small species (e.g., Nannippus) and the young of larger animals (e.g., Aphelops). The ducks (Anatidae) presumably fed on water plants and small invertebrates like its modern relatives, and probably were accompanied by one or more species of herons (Ardeidae) (a fossil heron is known from the nearby Withlacoochee River 4A Local Fauna [Becker, 1985; see chapter 2]). As stated in a previous chapter, the otter Enhydritherium was probably eating fish at this particular locality, though the heavy wear of this specimen's teeth indicate that previously it had at some past time consumed large numbers of hard-shelled invertebrates (presumably at a different locality, most likely along the coast). Unfortunately there is no good evidence to indicate what factors drew this animal to an isolated inland locality like Moss Acres Racetrack; however, whatever the attraction, its presence strongly suggests that the site had an abundant ichthyofauna. (It should be noted that this Enhydritherium individual had a severe pathology in its left ankle, and the resulting reduction in its mobility may have influenced its selection of Moss Acres Racetrack as either a temporary or permanent residence.)

The terrestrial fauna of Moss Acres Racetrack can potentially be divided into two major ecological categories, resident animals that lived permanently in the vicinity of the site, and migratory animals that were only present seasonally or irregularly. In modern African savanna communities browsers are mostly residents as are some grazers, while only grazers are migratory (Jarman and Sinclair, 1979). As stated above, the movement of migratory grazers in modern savannas is regulated by rainfall patterns and subsequent changes in grass productivity, the grazers spending the wet seasons in the open grasslands and the dry seasons in woodlands. One consequence of this pattern is a birth season for migratory grazers that typically coincides with the wet season; this allows young to spend their first months of life in a region where predation pressure is minimal and quality food is abundant (Bertram, 1979; see below). However, it should be pointed out that there are exceptions to this rule, such as the modern gemsbok (Oryx gazella) which is an aseasonal breeder despite being migratory (Smithers, 1983). As noted by Hulbert (1982), the age structure of a population at a fossil locality can be used to discern whether that population was migratory or sedentary; in the case of the Hulbert Neohipparion study, the presence of discrete age classes as well as the absence of probable neonates from the woodland Love site was interpreted as indicating a migratory lifestyle for this animal (see discussion of Aphelops in chapter 7). Thus, if this model is appropriate to Moss Acres Racetrack one would expect the neonates of migratory grazers to be almost completely absent from Moss Acres Racetrack, a presumed woodland locality like the Love site. For most of the taxa from Moss Acres Racetrack, there is insufficient material to determine reliably which of the numerous grazers found at the site might have been migratory and which sedentary on the basis of age class. However, a probable neonate is known for Cormohipparion emslei (see chapter 8), suggesting that this species may have been permanent or long term resident of the site (though the possibility that this species was an aseasonal breeder like the gemsbok cannot be ruled out). The relative abundance of juveniles in the Moss Acres Racetrack fauna suggests that the virtual lack of neonates is not primarily due to taphonomic factors, though it may be partly attributable to small sample size (for example, no neonates are known for either Amebelodon or Pliometanastes despite the fact that both animals were clearly browsers and hence presumably non-migratorial in the strict sense, though they may not have been sedentary). Thus, the migratory status of the Moss Acres Racetrack grazers must be considered to be currently unknown pending the discovery of further evidence.

If they are to avoid starving, mammalian carnivores must constantly stay in the vicinity of potential prey, with the result that their movements and distribution are inextricably linked to the movements and distribution of herbivores. One would intuitively expect medium to large mammalian carnivores be divided into two behavioral categories in modern African savannas: 1) individuals that seasonally wander back and forth between open grassland and woodland preying on the migratory grazers (and perhaps browsers in the woodlands), and 2) individuals that remain near woodlands and prey on non-migratory grazers and browsers year round, supplementing their diet with migratory grazers during the dry season. Contrary to expectations, however, only predators in the latter category exist in significant numbers in modern Africa. While a few carnivores may wander into the grassland after the migratory grazers during the wet season, the vast majority remain close to the woodlands permanently (reportedly due to low mobility of the dependent young). Thus, migratory grazers typically suffer almost no predation pressure during the wet season (Bertram, 1979).

The tentative conclusion that the habitat around Moss Acres Racetrack was a woodland with a population of resident herbivores (and perhaps migratory herbivores during the dry season) suggests that carnivores should have been relatively common at the site. Surprisingly however, terrestrial carnivores are extremely rare from the fauna, with only two Osteoborus orc individuals directly represented (probably too small to have preyed on the great majority of herbivores known in the fauna). In addition a gnawed juvenile Aphelops vertebra indirectly records the presence of carnivores in the fauna (see chapter 9). The gouge mark on this specimen is far too large to have been caused by the dentition of Osteoborus orc, suggesting that at least one more carnivore taxon must have been part of the fauna, perhaps a larger Osteoborus species (e.g., O. cynoides, known from the nearby and similarly aged Withlacoochee River 4X fauna).

This scarcity of carnivores in a fauna dominated by large herbivores, preserved in a facies that would have encouraged the herbivores to congregate (i.e., an apparent permanent watering hole), is counterintuitive, and must be explained. There are three possible explanations for a bias against carnivores in the collected fauna. (1) Terrestrial carnivores were present at this site in ordinary numbers, but the amount of material collected was insufficient to reveal them, carnivores tending to be vastly outnumbered by herbivores in mammal communities. (2) Taphonomic factors discriminated against the preservation of carnivores. And (3) for some reason carnivores were actually very rare in the original (as opposed to the collected) fauna, despite the abundance of potential prey.

Of these competing hypotheses the first, based on the small specimen sample size of the Moss Acres Racetrack fauna, is perhaps most plausible though it cannot be directly tested. As discussed at the end of the preceding chapter, simple chance can have a major impact on the known faunal diversity of a locality through sampling effects on rare taxa. Because of their location on the food pyramid carnivores are always rare in mammal communities, though because of either ecological and/or taphonomic biases they may in unusual cases be the most common component of some fossil assemblages (e.g., Rancho La Brea [Kurten and Anderson, 1980]). Therefore, just as some rare taxa, typically browsers, are known from Moss Acres Racetrack by sheer good luck (e.g., the tayassuid, antilocaprid, and "Pseudoceras" among others), by the same token many terrestrial carnivores originally present in the fauna may have been missed by simple bad luck. For example, without the recovery of the one gnawed Aphelops vertebra there would be no direct basis for surmising the presence of a large Osteoborus species like O. cyonoides in the fauna.

The small sample size hypothesis is challenged somewhat by the example of the carnivore fauna from the Withlacoochee River 4A site. As noted above, the Withlacoochee River 4A site resembles Moss Acres Racetrack in terms of its depositional facies, and includes a collection of specimens that is at least roughly similar in size to that of Moss Acres Racetrack based on a visual perusal (a direct count of specimens was not undertaken). Nevertheless, despite these similarities the Withlacoochee River 4A possesses a significant though not terribly diverse terrestrial carnivore fauna, including the bear *Indarctos*, the canids *Vulpes stenognathus*, *Osteoborus cyonoides*, and *O. orc*, and the sabercat *Machairodus*, with at least *O. orc* represented by numerous specimens. Though not ruling out sampling error, the Withlacoochee River 4A fauna suggests the possibility that some other hypothesis may explain the extreme rarity of terrestrial carnivores in the Moss Acres Racetrack fauna, stemming from taphonomic bias, ecological bias, or perhaps both in combination.

A simple taphonomic explanation for this situation appears implausible. Such an explanation would either require carnivores to be discriminated against preservationally over herbivores after dying within the site (an absurd proposition), or else require them to avoid the water much more often than herbivores. It is difficult to envision why the latter situation would occur, and indeed, if large herbivores were being mired within the site as argued in the preceding chapter, then one might well expect carnivores to be drawn into the site by their carcasses (this is the traditional explanation for the unusual abundance of carnviores in the Rancho La Brea fauna [Kurten and Anderson, 1980]).

An ecological bias against carnivores (i.e., an exceptional rarity in the fauna) is also rather implausible, though perhaps more plausible than a taphonomic bias. Such a bias would surely have its basis in carnivore habitat preference. As a woodland, Moss Acres Racetrack must have been either an isolated patch in an expanse of grassland, or else a part of a regional woodland with grassland in the vicinity. If Moss Acres Racetrack was an isolated patch of woodland, then the scarcity of terrestrial carnivores can be explained if one makes two assumptions: 1) the carnivores in this community stayed close to woodlands like their modern African counterparts; and 2) that Moss Acres Racetrack was so far from the larger woodlands inhabited by the carnivores as to have been outside their normal seasonal range. These assumptions pose difficulties, however. First, if Moss Acres Racetrack had been a mere island of woodland in a sea of grassland, then one would expect its fauna to have consisted almost entirely of grazers, a mere woodland patch being insufficient to support the browser fauna known from the site, particularly Amebelodon which would have swiftly destroyed it (see below). In addition, the presence of the giant otter Enhydritherium provides indirect evidence against Moss Acres Racetrack having been an isolated woodland patch. As was discussed earlier, Enhydritherium probably reached Moss Acres Racetrack by traveling a considerable distance overland (the possibility that it reached Moss Acres Racetrack by swimming a small stream connected to the locality cannot be ruled out; however, such a stream would probably have had a small gallery woodland associated with it, violating the premise invoked here that the Moss Acres Racetrack site was an isolated patch). If a relatively clumsy (at least in a terrestrial environment) and perhaps partially crippled Enhydritherium individual was able to cross the presumed grassland to reach Moss Acres Racetrack, then surely the more locomotively adept terrestrial carnivores could have done so as well.

Another possible explanation for an ecological bias against carnivores at Moss Acres Racetrack is that they had a distinct dislike for woodland habitats, implying the corollary that the modern African savanna is not a valid model for understanding carnivore paleoecology in the North American Miocene. In support of this position, Janis and Wilhelm (1993) argued on the basis of limb morphology that pre-Blancan terrestrial carnivores were ecologically very different from most of their modern relatives, with both pursuit predators like the cheetah [Acinonyx] and pack hunters like the African hunting dog [Lycaon] absent). However, this explanation is contradicted by the large carnivore fauna known from the Withlacoochee River 4A site discussed above. The Withlacoochee River 4A site was surely a woodland or forest locality (as indicated in part on the extraordinary abundance of the small browser "Pseudoceras" in the fauna) that was chronologically and geographically very close to Moss Acres Racetrack, the two localities separated only by about 33 kilometers (see chapter 2 and above). Thus, while savanna terrestrial carnivores may not have been particularly attracted to woodlands in north Florida (and perhaps North America) during the late Miocene, they clearly did not avoid them. Thus, with both taphonomic and ecological bias explanations largely discredited, sampling error remains as the most plausible explanation for the scarcity of terrestrial carnivores in the Moss Acres Racetrack fauna.

One of the most interesting aspects of the paleoecology of Moss Acres Racetrack is the terrestrial vertebrate community interrelationships. Unfortunately there is little or no information available about the terrestrial herpetofauna, avifauna, and carnivore fauna (see discussion above). Thus, community analysis of the Moss Acres Racetrack fauna must be largely restricted to the herbivores.

Small herbivores such as rodents and quite likely lagomorphs were part of the Moss Acres Racetrack fauna as indicated by their trace fossils (namely gnaw marks on bone; see chapter 9). However, their possible impact on the large herbivores in the community and the structure of the plant community is unclear. Most community studies of modern savannas have emphasized the role of large herbivores as keystone agents, completely neglecting the influence of small herbivores (e.g., Sinclair and Griffiths, 1979; Sarmiento, 1984; Bourliere and Hadley, 1970; and Owen-Smith, 1988). More research must be done on the role of rodents and other small herbivores in modern savanna communities before their role in the Moss Acres Racetrack or any other savanna paleocommunity can be assessed (assuming that modern tropical savannas can be used as an effective model for understanding the the Miocene savannas of North America).

An important aspect of community ecology is resource partitioning, particularly in regards to food, a subject already broached in the assignment of Moss Acres Racetrack herbivores to feeding guilds. Among mammalian herbivores, food resources are typically partitioned among species on the basis of the folowing factors: 1) the body size of the consumer; 2) the gut morphology of the consumer; and 3) the structure and nutritional quality of the plant consumed. Because of digestive and energetic factors, body size is positively correlated with the relative quality of the diet that can be tolerated by herbivores (e.g., the relative proportion of protein to lignin in a leaf) (Owen-Smith, 1988; see chapter 6). Thus, all other factors being equal, a relatively large herbivore can endure a lower quality diet than a small one. Dietary tolerance in herbivores has major consequences for their feeding behavior in terms of search patterns; since high quality food items tend to be much less abundant and more scattered than low quality ones, a relatively small herbivore must be more selective in searching for quality food items than a large herbivore (Janis and Ehrhardt, 1988).

Digestive tract morphology, specifically whether a given herbivore is a foregut or a hindgut fermenter, can also have a major impact on food choice. Foregut fermenters, with the ruminants serving as the chief example, are characterized by high digestive efficiency but relatively slow digestive rates (Owen-Smith, 1988). As a result, a given foregut fermenter must be careful to avoid an excessively low quality diet, lest the vegetation digest so slowly that the animal risks starvation with a full stomach. Hindgut fermenters in contrast, which include the majority of mammalian herbivores including perissodactyls and proboscideans, are characterized by relatively inefficient digestion but rapid digestive rates that allow a large amount of food to be passed per unit time irrespective of its nutritional quality. Because of this mode of digestion they can subsist on low quality vegetation unsuitable for foregut fermenters merely by eating it in huge quantities (Owen-Smith, 1988; MacFadden, 1992).

The degree to which a plant can be divided up among different herbivores for consumption is determined at least in part by its structural complexity, complex plants offering more discrete choices for herbivores than simple ones and thus reducing the need for resource overlap. For example, a typical woody tree offers to herbivores a crown with leaves and flowers/fruits at various heights, branches, trunk, and roots, while a grass merely offers a blade that can vary in height, flowers/fruits, and a root that may be either localized or wander a considerable distance as a runner. All other factors being equal therefore, in principle one would expect a forest to support a greater diversity of herbivores than a steppe, while a savanna as an intermediate stage between these habitats could support a greater diversity of herbivores than either a forest or a steppe alone, being able to support faunal elements of both habitats. Other factors may complicate this situation however, such as plant species diversity and a community-wide tendency for plant species to produce poor quality leaves (e.g., high in lignin content, defended by toxins, etc.) (Webb, 1987).

The browsing and mixed-feeding fauna of Moss Acres Racetrack is diverse but not a major part of the entire fauna in terms of total number of individuals represented, a common feature of savanna faunas (see above). Presumably these browsing/mixed-feeding taxa partitioned the non-herbaceous vegetation in a fashion so as to minimize competitive overlap, utilizing different structural components of the plant. For example, as stated above "Pseudoceras" was probably seeking the tenderest leaves, fruits and nuts, while the long-necked camelid Aepycamelus was surely seeking out leaves in the woodland canopy out reach of the other browsers. Of all of the browsers, Amebelodon was probably the most dietarily generalized, eating almost any kind of browse available including tree bark (Lambert, 1992). How the other browsers divided the non-herbaceous vegetation is not obvious, though presumably Pediomeryx fed on low level leaves and, using living members of the family as an example, the peccary quite possibly ate large numbers of fruits and seeds (Nowak and Paradiso, 1983), perhaps competing to some degree with "Pseudoceras."

Considering the apparent spatial and structural simplicity of a grassland, perhaps more intuitively surprising than the diversity of the browsers is the diversity of the grazers in this fauna, which includes at least nine horse species as well as tentatively the rhinoceros Aphelops (see chapter 7). A high grazer diversity is characteristic of many North American late Miocene savanna faunas, including in some cases perhaps as many as 13 species of horses alone (MacFadden, 1992). Thus, the ecological factors that supported a high diversity of grazers at Moss Acres Racetrack could well have been characteristic of many of the late Miocene savanna communities of North America (it should be noted however that as per Hulbert [1993] some of these taxa may not have been strict grazers, though they are unlikely to have been browsing specialists).

In modern African savanna communities, niche partitioning among grazers is largely based on three interrelated factors: seasonality in rainfall, temporal separation of potentially competing species, and regional differences in grass height and quality. In the Serengeti these factors all systematically influence herbivore behavior through a process called facilitative grazing or facilitation, with other processes occurring in other savanna communities such as the Ngorongoro Crater (Sinclair, 1979a; Eisenberg, pers. comm.; see below). The phenomenon of facilitative grazing can be summarized as follows. As discussed above, rainfall in savanna climates is strongly seasonal, and this seasonality has a strong impact on the growth pattern of the grass. During the dry season the grass away from permanent water sources is dormant, and as a consequence the migratory grazers take refuge near woodlands. With the onset of the rains however the grass undergoes explosive growth, and quickly forms an expanse of relatively tall, low quality vegetation. Because of its low quality this initial growth is available only to hindgut fermenters and very large foregut fermenters, and as a consequence zebras (the most dietarily tolerant of the migratory grazers) leave the woodland refuge and return to the grassland, consuming the coarsest growth. After the zebras have removed the coarsest growth in a given region they move on in search of an ungrazed region, to be followed by the wildebeest. The wildebeest are also dietarily tolerant, and systematically reduce the still relatively tall grass left by the zebra to either a medium height or a short but active sward. The grass responds to this grazing through the production of new, high quality growth, and this growth is consumed by smaller migratory foregut fermenters such as the topi (Damaliscus lunatus) and the Thomson's gazelle (Gazella thomsoni). The topi reduces medium height grass left by the wildebeest to a short sward, while the Thomson's gazelle follows the wildebeest and/or the topi, looking for particularly nutritious patches of grass in short sward. With the end of the rainy season the grazers return to the woodland refuge, completing the cycle (Maddock, 1979).

Facilitative grazing is a potential explanation for the diversity of apparently sympatric grazers found at the Moss Acres Racetrack and other late Miocene savanna communities. Rather than simultaneously competing for grass in the same locality, groups of grazers would have moved through regions in separate waves, each wave altering the grass structure so as to (inadvertantly) make it more suitable for the wave behind. If a version of facilitative grazing was a major influence on the savanna of north Florida, then one would in principle expect its grazing fauna to have had the following attributes based on analogy with the modern African Serengeti fauna: 1) a migratory component; 2) a division into distinct body size classes, each class corresponding to a facilitative wave; 3) dietary segregation among the migratory grazers consistent with their body size classes; and 4) an abundance of individuals in the size classes consistent with the facilitation process (e.g., the facilitative grazing could not be maintained if presumed secondary and tertiary grazers outnumbered the primary grazers).

As discussed above, the evidence for migratorial taxa in the Moss Acres Racetrack fauna is ambiguous, with limited evidence of migratorial status existing only for the species _Cormohipparion_ _emslei_. If we are to explore the possibility of facilitation in the vicinity of the Moss Acres Racetrack site further, we must make the tacit assumption that at least some of the Moss Acres Racetrack grazers were migratory, an assumption that is allowable by virtue of there being no evidence against it. However, any inferences in favor of facilitative grazing that are drawn from this exploration must be tempered by the fact that a key aspect of the process, migratory behavior, remains unverified.

Body size clumping is a major aspect of the modern facilitation process. It has its basis in the need for sympatric grazers to avoid excessive overlap in food resources, a continuum of body sizes requiring an unrealistically fine partitioning of grass height levels (see the discussion of Hutchinsonian ratios below). A faunal list of grazing ungulates in the Serengeti community, including their body masses and migratory statuses, is presented in Table 10-3. This data is presented graphically in Figure 10-1. A distinct tendency towards body mass clumping is clearly visible when this data is looked at as a whole, and this tendency is particularly evident when migratory grazers are considered alone. The zebra (Equus burchelli), wildebeest (Connochaetes taurinus) and the gemsbok (Oryx gazella) constitute a distinct size clump and consume very to moderately tall grass, reducing it to a medium or low level. The next smaller size clump, including the topi (Damaliscus lunatus) among the migratorial grazers, feeds on the medium height grass left by the wildebeest and gemsbok and reduces it to a low level, while the Thomson's gazelle feeds on the short grass left by the migratory grazers in either of the aforementioned size clumps (Jarman and Sinclair, 1979). In

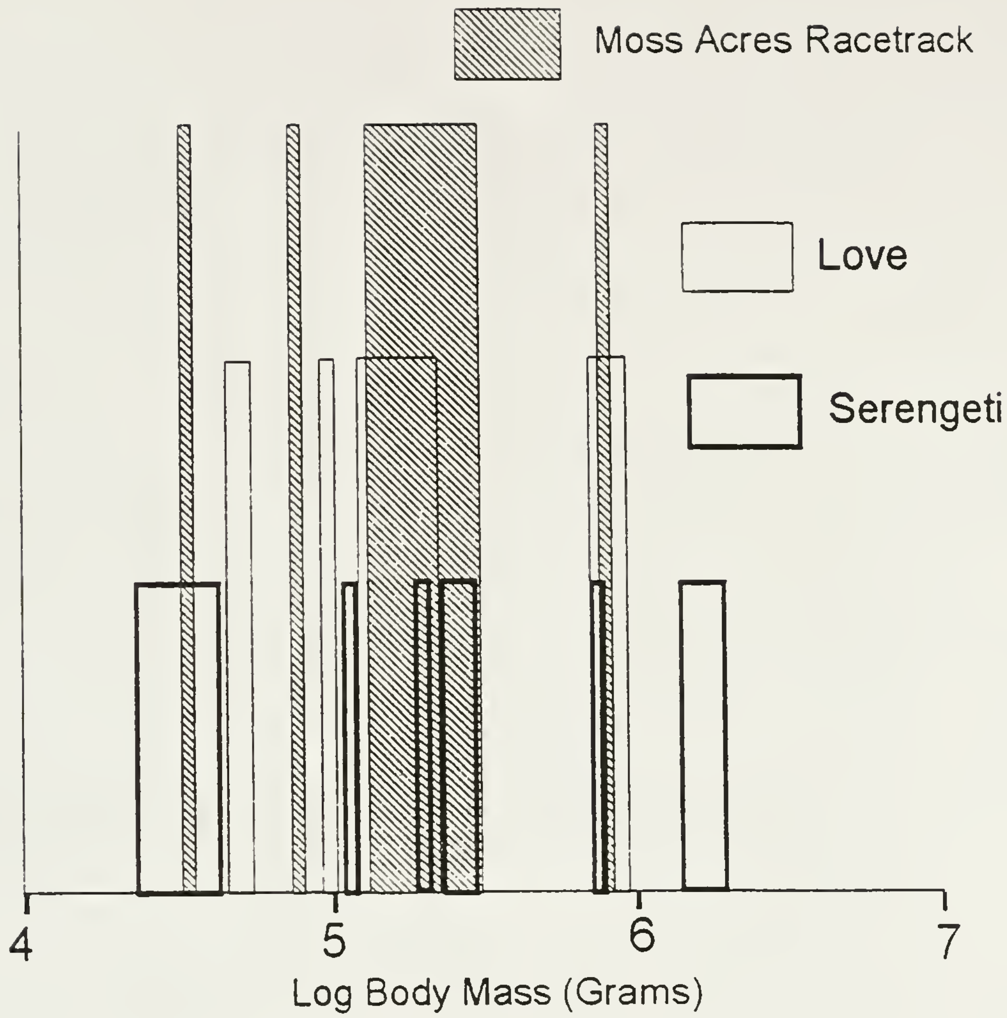

Figure 10-1. Graphical portrayal of clumped body mass distributions (log mass in grams) for grazers in the Moss Acres Racetrack, Love, and Serengeti faunas. Note that the Y-axis is scaleless, differences in clump height between the different faunas constituting a visual aid only.

Table 10-3. Body masses (kg) of ungulate grazers (excluding mixed-feeders) in the modern African Serengeti community arranged from smallest to largest (faunal list compiled from Sinclair and Griffiths, 1979; body mass values compiled from Smithers, 1983 and Holling, 1992; and migratorial status data compiled from Nowak and Paradiso, 1983, Sinclair and Griffiths, 1979, and Smithers, 1983).

Species	Body Mass	Clump No.	Migratory Status*
Gazella thomsoni	23	1	migratory
Redunca redunca	43	1	non-migratory
Damaliscus lunatus	133	2	migratory
Alcephalus buselaphus	136	2	non-migratory
Connochaetes taurinus	215	3	migratory
Oryx gazella	225	3	migratory**
Kobus ellipsiprymnus	260	4	non-migratory
Hippotragus equinus	270	4	non-migratory
Equus burchelli	308	4	migratory
Syncerus caffer	775	5	non-migratory
Hippopotamus amphibius	1406	6	non-migragory
Ceratotherium simum	1825	6	non-migratory

*: The term migratory indicates systematic movement in response to seasonal changes in rainfall, while the term non-migratory indicates either unsystematic movement or else long term residency at a locality.

**: aseasonal breeder.

order to determine whether the Moss Acres Racetrack grazing fauna can be divided into distinct body size classes, one must first derive estimates of body mass for the species. Directly measuring the mass of fossil vertebrates is impossible, and thus this feature must be estimated on the basis of comparison with living animals, in most cases by means of regressions based on modern specimens. Raw data for estimating the body masses of Moss Acres Racetrack mammals are presented in Table 10-4, including both grazers and non-grazers for the sake of completeness (Hipparion cf. tehonense, the unidentified pecarry, the camelids, "Pseudoceras," and the unidentified antilocaprid are excluded because of a lack of specimens suitable for estimating body mass). Where possible, masses were estimated using more than one specimen and more than one regression. The regression equations used and their average predictor errors for modern taxa used in the regression are presented in Table 10-5. Regression equations were chosen so as to minimize the average predictor error when one was available, with no equations chosen having a predictor error greater than 30 percent.

The actual body mass estimates of the Moss Acres Racetrack grazers are presented in Table 10-6, with the estimate considered to be the midpoint of the size range. Even assuming a healthy margin for error in the estimates, body mass clumps are clearly visible in the distribution (the average mass for each clump is presented in Table 10-8) (see

Table 10-4. Raw body mass data for mammals in the Moss Acres Racetrack fauna (all measurements in centimeters, square centimeters, or kilograms).

Grazers:

Aphelops mutilis
tibia, UF 69976, T2= 11.5
tibia, UF 90300, T2= 10.5
humerus, UF 90300, H2= 40.3, H3= 10.2
estimated masses: 591, 456 (T2), 1000 (H2), 1071 (H3)

Hipparion cf. *tehonense*
no suitable specimens available for estimating a body mass

Neohipparion eurystyle
mandible, UF 69969, FLPA= 2.52, LMRL= 6.3
estimated masses: 172 (FLPA), 159 (LMRL)

Calippus mccartyi
skull, UF 69951, SUMA= 2.56
estimated mass: 73

Cormohipparion emslei
mandible, UF 97259, FLPA= 2.66
estimated mass: 186

Cormohipparion plicatile
mandible, UF 103754, TLML= 2.2, LMRL= 7.0
estimated masses: 155 (TLML), 219 (LMRL)

Nannippus aztecus
femur, UF 69954, F2= 24.8
mandible, UF 69933, FLPA= 1.20
estimated masses: 101 (F2), 57 (FLPA)

Nannippus morgani
isolated M2, SUMA= 1.56
estimated mass: 36

Dinohippus sp.
skull, UF 95399, SUMA= 7.20
estimated mass: 330

cf. *Astrohippus*
humerus, UF 97270, H1= 22.1
estimated mass: 225

Table 10-4--continued

Non-grazers:

Enhydritherium terraenovae
humerus, UF 100000, Ch= 4.8
femur, UF 100000, Cf= 4.7
estimated mass: 21

Osteoborus orc (specimen from the Withlacoochee River 4A)
mandible, UF 13180
LM1= 2.3
estimated mass: 18

Pliometanastes protistus
femur, UF , Cf= 17.7
estimated mass: 219

Amebelodon britti
femur, UF 69997, Cf= 41.7
femur, UF 69999, Cf= 42.8
estimated mass: 10,048

"*Pseudoceras*" (specimens from the Withlacoochee River 4A)
humerus, UF 13827, H4= 1.7, H5= 1.7
humerus, UF 18953-15, H4= 1.5, H5= 1.6
humerus, UF 18593-18, H4= 1.5, H5= 1.6
femur, UF 18957-1, F2= 3.0, F5= 2.2
femur, UF 18957-5, F2= 3.2, F5= 2.3
estimated masses: 10.26 (H4), 6.87 (H5), 11.22 (F2), 8.68 (F5)

abbreviations: Cf= femoral circumference; Ch= humeral circumference; FLPA= fourth lower premolar area; F2= distance between the greater and lesser trochanters; F5= distance from medial condyle foramen to outermost edge of lateral condyle; H1= humeral length from the lesser tubercle; H2= humeral length from the greater tubercle; H3= maximal mediolateral width of the humeral head; H4= minimal width across the humeral trochlea; H5= maximal width across the humeral trochlea; LM1: antero-posterior length of m1; LMRL= lower molar row length; LPRL= lower premolar row length; SUMA= second upper molar area; T2= maximal mediolateral width across the proximal tibia end; T3= anteroposterior length of the medial articulating surface of the proximal end of the tibia; TLML= third lower molar length. See Table 10-3 for associated regression equations.

Table 10-5. Regression equations used to estimate grazer body masses (all regrssions yield masses in kilograms).

Regression Equation	P.E.	Source
Cf+Ch: BM= $0.000084(\mathrm{Ch+Cf,\ mm})^{2.73}$	none	Alexander, 1989
Cf: BM= $.00016(\mathrm{Cf,\ mm})^{2.73}$	none	Alexander, 1989
Cf, el: BM= $0.000397(\mathrm{Cf,\ mm})^{2.827}$	26	Roth, 1990
F2,eq: logBM= 2.981 log(F2,cm)-2.154	20	Scott, 1990
F2, rum: logBM= 2.7237 log(F2, cm)-0.2882	20	Scott, 1990
F5, rum: logBM= 2.9006 log(F5, cm)-0.0830	22	Scott, 1990
FLPA, eq: logBM= 1.491 log(FLPA,cm) +1.637	20	Janis, 1990
H1, eq: logBM= 2.879 log(H1, cm)-1.518	16	Scott, 1990
H2, eq: logBM= 2.714 log(H2, cm)-1.357	27	Scott, 1990
H3, eq: logBM= 2.656 log(H3, cm)+.351	16	Scott, 1990
H4, rum: logBM= 2.5518 log(H4, cm)+0.4903	19	Scott, 1990
H5, rum: logBM= 2.6372 log(H5, cm)+0.2574	19	Scott, 1990
LM1, can: logBM= 1.87 log(LM1, mm)-1.22	27	Van Valkenburgh, 1990
LMRL, eq: logBM= 3.061 log(LMRL, cm)-0.246	22	Janis, 1990
SUMA, eq: logBM= 1.456 log(SUMA, cm) +1.270	29	Janis, 1990
T2, ung: logBM= 2.849 log(T2, cm)-0.250	21	Scott, 1990
TLML, eq: LogBM= 2.999 log(TLML, cm) +1.162	18	Janis, 1990

abbreviations: BM= body mass, can= canids, el= elephants, eq= equids, rum= ruminants, ung= all ungulates; P.E.= mean percentage predictor error within modern animals used to obtain the regression. See Table 10-2 for explanation of other abbreviations.

Table 10-6. Estimated body masses (kg) of the grazers in the Moss Acres Racetrack Local Fauna arranged from smallest to largest.

Taxon	Body Mass Estimate Range	Body Mass Midpoint	Clump Number
Nannippus morgani	36	36	1
Calippus mccartyi	73	73	2
Nannippus aztecus	57-101	79	2
Hipparion cf. *tehoense*	-----	151*	3
Neohipparion eurystyle	159-172	166	3
Cormohipparion emslei	186	186	3
Cormohipparion plicatile	155-219	187	3
cf. *Astrohippus*	225	225	3
Dinohippus sp.	330	330	3
Aphelops mutilis	456-1071	764	4

*: value taken from MacFadden and Hulbert (1990)

Figure 10-1). *Nannippus morgani* clearly forms a distinct clump of its own, being by far the smallest grazer in the fauna at 36 kilograms. The next clump contains two species, *Calippus mccartyi* and *Nannippus aztecus*, with an average mass of 76 kilograms. The third clump includes *Hipparion* cf. *tehoense*, *Neohipparion eurystyle*, *Cormohipparion emslei*, *Cormohipparion plicatile*, cf. *Astrohippus*, and *Dinohippus* with an average value of 208 kilograms, while the fourth clump contains *Aphelops mutilis*, which at 764 kilograms is more than three times the average mass of the third clump.

It is clear that the body masses of the Moss Acres Racetrack grazers are not distributed in an even, continuous fashion even if one takes into account clearly present estimate errors. However, this discontinuity may be the result of random chance alone. To determine the statistical plausibility of these clumps, the Moss Acres Racetrack grazer mass distribution was subjected to a cluster analysis using the program Number Cruncher Statistical System (NCSS) 5.01 (Hintze, 1987). The cluster analysis failed to reveal any significant clumps in this distribution, two clusters accounting for a mere 19.89% of the variation with the values being much lower for greater numbers of clusters. As an independent test of this methodology the mass distribution of the Serengeti grazers with its known, biologically meaningful clumps was subjected to the same analysis. The results of this analysis were similar to those for Moss Acres Racetrack, two clusters accounting only for 13.4% of the variation.

Unfortunately the statistical analysis of univariate clumps in body mass distributions is currently in a pioneer stage, with no currently established methodologies (Sendzimir, pers. comm.). Thus, for the moment one must accept the existence of these clumps without the benefit of rigorous statistical verification.

Body masses were also estimated for the ungulates of the Love site fauna by MacFadden and Hulbert (1990), and the values for the grazers are presented in Table 10-7. Like the Moss Acres Racetrack fauna the body mass distribution of the Love grazers is divisible into four distinct clumps, whose average values are presented in Table 10-8. The clump distribution of the Love grazing fauna is crudely similar to that of Moss Acres Racetrack (see Figure 10-1), the two not being distinguishible at a significance level of 5% under a chi-squared goodness of fit test.

Both the Moss Acres Racetrack and Love grazing faunas have significantly clumped body mass distributions, a finding that is consistent with these faunas having been involved in facilitative grazing. However while a prerequisite, this finding is not a logical proof of facilitative grazing, body mass clumping having other possible explanations. For example, Holling (1992) proposed that body mass clumping is a fundamental aspect of all terrrestrial mammal and bird communities, the clumps resulting from a strong discontinuity in the scale of habitat structure. Thus, one must look at additional lines of evidence to plausibly show that

Table 10-7. Estimated body masses (kg) of the grazers in the Love Local Fauna arranged from smallest to largest (values taken from MacFadden and Hulbert [1990]).

Taxon	Estimated Mass	Clump Number
Calippus elachistus	49	1
Pseudhipparion skinneri	61	1
Nannippus westoni	93	2
Calippus cerasinus	102	2
Cormohipparion ingenuum	139	3
Neohipparion trampasense	142	3
Hipparion cf. *tehoense*	151	3
Protohippus gidleyi	204	3
Cormohipparion plicatile	214	3
Teleoceras proterum	635	4
Aphelops malacorhinus	889	4

Table 10-8. Body mass (kg) clump distribution in the grazing faunas of the Moss Acres Racetrack site, Love site, and the modern African Serengeti.

Site/Fauna	Clump Number	Average Clump Mass	No. of Taxa in Clump
Moss Acres Racetrack	1	36	1
	2	76	2
	3	208	6
	4	764	1
Love	1	50	2
	2	99	2
	3	170	5
	4	762	2
Serengeti	1	33	2
	2	135	2
	3	220	2
	4	279	3
	5	775	1
	6	1616	2

facilitative grazing was practiced by members of the Moss Acres Racetrack fauna.

Dietary selectivity is a fundamental aspect of the facilitation process, a succeeding wave of grazers being more selective than the preceding wave by virtue of a lower dietary tolerance. Among living ungulates, relative dietary selectivity is strongly correlated with muzzle (premaxilla) shape. Nonselective feeders tend to have broad, "squared-off" muzzles for taking large indiscriminant bites of vegetation, while more selective feeders tend to have narrower, more tapered muzzles. Thus, a Thomson's gazelle has a relatively narrower, more tapered muzzle than a wildebeest despite the fact that both animals are grazers. There is a degree of scatter in this trend; for example, despite being larger and typically the first grazer in the facilitation wave, the muzzle of a zebra has a narrower profile than that of a wildebeest. Nevertheless, there is no doubt but that in the modern Serengeti fauna unselective, tall grass grazers have broader muzzles than the more selective, short grass grazers (Janis and Ehrhardt, 1988).

Using the modern Serengeti as a model, one would expect that the large, presumably tall grass grazers in the Moss Acres Racetrack fauna to have broad, squared-off muzzles and the smaller grazers to have relatively narrow, tapered muzzles if facilitation was practiced. Unfortunately however, the situation is not clearcut. Muzzle profile is evidently of little value in determining feeding behavior in rhinoceroses such as *Aphelops* (see chapter 7). The other grazers in the fauna are horses, and with one exception noted below all are characterized by muzzle profiles consistent with generalized grazing, with no preference for a particular grass length indicated (MacFadden, 1992). Thus, there is no morphological evidence that the small horse *Nannippus morgani* was more selective in its diet than the large horse *Dinohippus*, a finding inconsistent with expectations for a facilitating fauna. The only horse in the fauna with a muzzle profile consistent with a dietary specialization is *Calippus mccartyi*, which has the broad, squared-off muzzle indicative of an unselective grazer. Surprisingly however *Calippus* is not a large grazer but rather one of the smallest members of the fauna, belonging to the second body size clump. The subgenus *Cormohipparion* (*Notocradhipparion*) which includes two speces in the fauna, *C*. (*N*.) *emslei* and *C*. (*N*.) *plicatile*, is not characterized by a specialized muzzle profile like *Calippus*, but does have a much wider mandibular diastema than that found in any other hipparionine (Hulbert, 1988b; see chapter 8). The functional significance of this wide diastema is uncertain, but if modern ruminants are used as an analog then it implies that the tongue of these animals was used to manipulate vegetation to a greater degree than typical horses, which strictly crop grass with their incisors. Whatever the functional explanation, the wide diastema of these two species suggests that like *Calippus* they were involved in specialized feeding behavior, and thus may have had more selective diets than the other equids.

The lack of a clear pattern of dietary selectivity among the Moss Acres Racetrack grazers argues against facilitative grazing having been practiced by this fauna, dietary selectivity being a fundamental aspect of the process. However, another factor must be considered before any conclusions are drawn from these results. With the lone exception of the equid zebra, all of the grazers involved in facilitation in the savannas of modern Arica are foregut fermenters, while in the Moss Acres Racetrack fauna all of the grazers are hindgut fermenters. As was discussed above, foregut fermenters are very sensitive to dietary quality, particularly in regards to body size considerations; thus, a Thomson's gazelle could never tolerate the poor quality diet typically consumed by a wildebeest. However, hindgut fermenters are relatively insensitive to dietary quality, with body size being a relatively unimportant factor; for example, most voles have diets consisting largely of grass despite their diminutive size, with one species known to be specialized for a diet of pine needles (Krebs, 1984). Thus, comparing the Moss Acres Racetrack grazing fauna to a fauna from modern Africa is in effect comparing apples and oranges. The dynamics governing facilitation in modern Arican savanna communities, with their dominance by foregut fermenters, are likely to be very different from those governing a savanna community of hindgut fermenters considering the more uniform dietary tolerance in the latter.

Considering that modern facilitation is largely based on a gradient in dietary tolerance among the grazers, one is justified in questioning whether there is any basis for facilitation in a community of hindgut fermenters. The modern example of the voles as well as the apparent nonselective grazing of the small horse Calippus mccartyi demonstrates that small hingut fermenters are quite capable of consuming poor quality fodder, with the implication therefore that in this situation large grazers would not in principle have changed the environment to the benefit of the small ones (i.e., "facilitated"). However, one must also consider the fact that modern facilitative grazing does not merely regionally change food quality, but also habitat structure. Grass height influences an animal's locomotion and visibility on the basis of its body size (e.g., a Clydesdale horse could move more easily and see farther in a tall grassland than a miniature horse). This effect has been documented for the Thomson's gazelle, which has considerable difficulty dealing with the tall grass present in the early wet season (Kingdon, 1971). Therefore, facilitative grazing cannot be discounted for the Moss Acres Racetrack fauna merely because (like most late Miocene presumed savanna faunas in North America) it was dominated by hindgut fermenters, though this modified version of facilitation may have generated more loosely structured body mass clumping than that formed by the modern process.

Facilitative grazing, whether driven by dietary or structural factors, is inherently based on gradations in body size, large grazers systematically creating conditions suitable for smaller ones. In any facilitative system one would in principle expect the primary grazers to be at least roughly as numerous as the members of the following size classes if not more numerous, since they are the primary agents of habitat modification. In agreement with this premise, the primary grazing class of the modern Serengeti includes more individuals than any other size class, particularly the wildebeests (Sinclair, 1979a). Thus, if the Moss Acres Racetrack grazing fauna was involved in facilitation, one would expect that the primary grazers were at least a major if not a dominant part of the fauna. Unfortunately, the total amount of material recovered from the Moss Acres Racetrack site is insufficient to estimate the relative abundances of the various size classes in the fauna. However, trends have been observed at the regional level for the late Miocene across North America, and Moss Acres Racetrack can be encompassed within these observations.

The equid fauna of North America was not homogeneous during the late Miocene, but rather showed distinct regional variation. For example, large monodactyl horses like Dinohippus dominated Great Plains faunas during the Hemphillian, while those of the Gulf Coastal Plain were dominated by smaller three-toed horses (MacFadden, 1992; Shotwell, 1961). Taken at face value, this pattern suggests that facilitation was a more important phenomenon in the Late Miocene Great Plains than the Gulf Coastal Plain. However, this conclusion is based on the unstated premise that small body size made even the largest three-toed horses poorly suited for primary grazing compared to the larger monodactyl horses, a premise that is open to debate. Though the zebra is an important ecological agent in the modern Serengeti, the facilitation process in this community is primarily driven by the much smaller but more abundant wildebeest (Maddock, 1979), an animal similar in size to the largest three-toed horses in both the Moss Acres Racetrack and Love faunas. If the zebra were to be greatly reduced in numbers or even completely exterminated from the Serengeti, in all likelihood facilitation would still continue in some fashion. Similarly, some form of facilitation could have been driven by the largest three-toed horses in the late Miocene Gulf Coastal Plain (e.g., _Cormohipparion_ _plicatile_ in both the Love and Moss Acres Racetrack faunas, the equine _Protohippus gidleyi_ in the Love fauna [see Tables 10-6, 10-7, and 10-8) even if large monodactyl horses were present only in low numbers.

In conclusion, the case for facilitative grazing by the Moss Acres Racetrack fauna (as well as other late Miocene Gulf Coastal Plain faunas such as the Love) is ambiguous. No line of evidence examined so far, including body size distribution, dietary selectivity, and numbers of individuals within size classes has convincingly supported or refuted facilitation. It is conceivable that future evidence will allow this question to be addressed more directly; for example, it may become possible to distinguish facilitative waves on the basis of subtle isotopic clues (see Hulbert, 1993) Studies of a large number of grazing taxa in other faunas like that performed by Hulbert (1982) for Neohipparion may demonstrate large scale migratory behavior, and thus by implication facilitation, at other localities. In conclusion, however, it should be noted that circumstantial ecological evidence favors facilitation in some form having occurred at Moss Acres Racetrack and quite likely over much of North America as well. The Moss Acres Racetrack fauna contained at least 10 regionally sympatric species that depended on grass, though possibly to varying degrees. This structurally simple resource could have been effectively partitioned among so many consumers without creating severe competition only if the consumers were separated in time and space in an orderly fashion, a natural result of facilitation.

The Moss Acres Racetrack body mass data presented in Table 10-6 allows an ecological issue other than facilitation to be examined, namely Hutchinsonian ratios. Hutchinson (1959) proposed that when ecologically similar species (usually but not necessarily congeners) coexist sympatrically, they are generally separated in body size by a factor of 2.0-2.2 in order to minimize niche overlap (note that the reality and biological significance of Hutchinsonian ratios have been disputed; see Maiorana, 1990 and MacFadden and Hulbert, 1990). Two genera in the fauna, *Cormohipparion* and *Nannippus*, are represented by two species, and thus allow for a check of the validity (though not necessarily the significance) of this principle. The two *Nannippus* species, *N. morgani* and *N. aztecus*, are separated in body mass by a factor of 2.19 (79 kg:36 kg) and thus are consistent with Hutchinson's rule. However, *Cormohipparion plicatile* and *C. emslei* have essentially indistinguishable masses (187 kg:186 kg); even if a significant margin for error is added to these estimates (e.g., a range of 155-215 kg for *C. emslei*), their similarity still is great enough to clearly violate Hutchinson's rule. One must therefore conclude that either this situation disproves the universal validity of Hutchin's rule, or else some fundamental premise of Hutchinson's rule has been violated. It is impossible to prove which of these explanations is correct with current data. However, there is modern precedent for the second explanation. The topi (*Damaliscus lunatus*) and hartebeest (*Alcephalus buselaphus*) are sympatric grazers in the Serengeti fauna with approximately the same body size (see Table 10-3), but they generally do not compete intensively because the topi is migratory and the hartebeest a woodland resident. Thus, in this case significant ecological differences between these two apparently similar species violate an important premise of the Hutchinson hypothesis. Admittedly this example does not directly reflect the situation represented by Cormohipparion emslei and C. plicatile, since the topi and hartebeest are not congeners. However, differences of a similar nature are known in modern congeners; for example, Thomson's gazelle is a grazer and Grant's gazelle a mixed feeder despite both animals being congeners and fairly close in size (Smithers, 1983), allowing them both to potentially coexist without strictly violating Hutchinson's rule. Returning to the apparent violation of Hutchinson's rule by Cormohipparion emslei and C. plicatile, this situation can be explained if one assumes (admittedly without direct evidence) that these two species were ecologically distinct in a fashion unrelated to body size (it should be noted that both of these species possess a wide diastema, an apparent feeding adaptation unique within the hipparionines that renders this proposal particularly tenuous).

There has already been considerable discussion of possible plant-animal interactions at the Moss Acres Racetrack site, particularly in regards to grass and grazers. However, one possible interaction that has been so far neglected but worthy of mention is the possible interrelationship between the savanna biome and Amebelodon and other late Miocene proboscideans. In modern African savannas the African elephant can be thought of as a "mobile ecological disturbance," consuming and destroying large numbers of trees when foraging in the vicinity of woodlands, though the woodlands themselves are actually destroyed and converted into grassland only under unusual conditions. This consistent (though not necessarily continuous) disturbance of woodland has two major ecological effects: 1) a canopy is strongly discouraged, forcing the woodland to remain open, and 2) a stable successional state that would exclude colonizer species is never reached, so that plant diversity is enhanced. These effects, in turn, affect the associated fauna in the following manner: 1)due to the significantly greater ground insolation resulting from the absence of a canopy, the amount of food available for low to the ground terrestrial herbivores is greater than it would be otherwise, and 2) the increased plant diversity allows for the possibility of finer niche partitioning than would be possible otherwise, and hence a greater supportable herbivore diversity. Because of its major ecological impact on the savanna community as a whole, the African elephant can be considered a prime example of a keystone species (Owen-Smith, 1988).

Lambert (1992) studied the feeding behaviors of a number of gomphotheres, including _Amebelodon_, by examining wear patterns on both their upper and lower tusks. In this study Lambert found strong evidence that _Amebelodon_ and other gomphotheres were feeding extensively on trees, particularly their bark, much like modern African elephants. In particular, he documented wear patterns on _Amebelodon britti_ upper tusks consistent with tree foraging (see chapter 3).

Assuming that the evidence has been interpreted correctly, it would appear that Amebelodon and the other assorted gomphotheres (possibly including mammutid proboscideans as well) were ecologically analogous to the modern African elephant, in all likelihood acting to restrict the spread of woodlands in the late Miocene savannas of North America. As in the modern African savanna, this would probably have had the effect of enhancing the potential floral and faunal diversity of the region. For example, it is possible that the diversity of ungulates, particularly horses, in the Moss Acres Racetrack region would have been much lower if Amebelodon had not created a mosaic of successional habitats. The extinction of Amebelodon in the late Hemphillian may have been caused by landscape homogenization as woodlands were lost to encroaching grassland, an event that may have secondarily reinforced that same landscape homogenization and hastened the extinction of other animals dependent on the heterogeneous savannas.

CHAPTER 11
SUMMARY AND CONCLUSIONS

Major aspects of the Moss Acres Racetrack site have been studied and discussed in the preceding chapters, including the geology, taphonomy, fauna, palynoflora, climate, and community ecology. The results of these studies are summarized below, with concluding remarks following.

Geology

The Moss Acres Racetrack site represents a clay-filled sinkhole formed in limestone from two sources, the Miocene Hawthorn and Eocene Ocala Limestones. The formation represented by the clay is inconclusive, but evidence indicates it is related to the geological complex referred to as the Alachua Formation. The clay is composed of a nearly pure combination of kaolinite and illite with heavy contaminants like phosphate, zirconium, and garnet absent, indicating that this sediment is most likely the result of *in situ* sediment weathering under relatively quiescent conditions. However, the preservation of peat and pollen in the clay suggests that this weathering occurred *ex situ* and therefore that the sediment must have been deposited in some fashion, though the exact mechanism for this deposition is unclear. The fine nature of the clay and the complete absence of sand from the fossiliferous units argues that the deposition having occurred under continuous fluvial conditions.

Taphonomy

The Moss Acres Racetrack site is characterized taphonomically by the following features: 1) an extraordinary abundance of articulated/associated specimens; 2) a bias towards the preservation of isolated associated limb elements; 3) a near absence of pre-burial modification of bones by such means as gnawing or trampling; and 4) a near absence of a microfauna, including fish, amphibians, reptiles (i.e., lizards and snakes), and mammals such as rodents. Orientation data on a sample of long bones provides no evidence of a directional bias consistent with exposure to a significant current, though the orientation patterns appear far from random (possibly a statistical anomaly resulting from the small data set examined). These data are interpreted as indicating a general lack of transport of specimens, the animals having apparently died immediately within or in some cases adjacent to the site (this finding is consistent with the geological evidence). The bias towards isolated limbs is explained as a result of miring, the legs of animals being buried by passive sinking into the sediment while the associated torso rots off and floats away or disarticulates. The absence of microfossils is explained by both their inability to sink into the sediment under their own weight, and a rate of fluvial deposition too slow to bury them before their destruction.

Fauna

Though mammals dominate the fauna in terms of diversity, large reptiles comprise an important component of the fauna. Turtles are common, including the genera *Geochelone*, *Apalone*, *Trachemys* (possibly the earliest record for this genus) and *Pseudemys* (possibly representing a new species). *Alligator* is also abundant, possibly representing a new species distinct from both *A mississippiensis* and *A. olseni*.

Among the mammals, horses are the most common and diverse group (studied in depth elsewhere by Richard Hulbert), including seven genera (*Astrohippus*, *Dinohippus*, *Calippus*, *Nannippus*, *Cormohipparion*, *Neohipparion*, and *Hipparion*) and nine species (*Astrohippus* sp., *Dinohippus* sp., *Calippus mccartyi*, *Nannippus aztecus*, *N. morgani*, *Cormohipparion emslei*, *C. plicatile*, *Neohipparion trampasense*, and *Hipparion* sp.). The rhinoceros *Aphelops mutilus* is also extremely abundant, with juveniles a surprisingly large part of the fauna. Analysis of the limited data available suggests that this animal was a grazer like the horses. The gomphothere proboscidean *Amebelodon britti* (described as a new species with the holotype collected from Moss Acres Racetrack) is a major component of the fauna, representing one of the largest single assemblages for this genus in the world (rivaled only by the Rhinoceros Hill Quarry in Kansas). Three skulls of this animals were collected from Moss Acres Racetrack (as yet unstudied), the first referable to this genus ever collected in reasonably good condition. Most of the other mammal taxa in the fauna are represented by relatively small samples, though many are of outstanding quality. A nearly complete skeleton of the otter *Enhydritherium terraenovae* represents the most complete bunodont otter specimen known in the world, and allowed the osteology, functional morphology, and ecology of this species to be studied at a detailed level impossible for this species before (a phylogenetic analysis led to inconclusive results). An associated forelimb and hindlimb referable to the ground sloth *Pliometanastes* sp. allowed osteological features of many limb elements to be observed for the first time for this genus. Comparison of this material with that from the older (very early Hemphillian) McGeehee fauna reveals subtle differences that could indicate anagenetic evolution within this lineage. Material referable to the dromomerycid ruminant *Pediomeryx* includes a partial skull with intact horn cores, the first ever observed in this species. Other mammal taxa in the fauna are represented by relatively scant and unremarkable material, including an unidentified peccary, a long-necked camelid (probably *Aepycamelus*), the llama *Hemiauchenia*, a hornless ruminant near *Pseudoceras*, an unidentified antilocaprid, and a single terrestrial carnivore, the small bone-eating dog *Osteoborus orc*.

Flora

The palynoflora of Moss Acres Racetrack is dominated by unidentified grasses and oaks, with a number of other taxa individually comprising only a relatively minute portion. In its overall character the Moss Acres Racetrack flora resembles that of a modern woodland in the southeastern United States, with exotic tropical taxa absent.

Climate

Both faunal and palynological evidence indicates that northcentral Florida, and in all likelihood southeastern North America as a whole, were subject to a climate with the following attributes: 1) a temperature seasonality and range similar to that found in the region currently, roughly warm temperate (subtropical on the Koeppen classification system); and 2) a rainfall pattern showing strong seasonal aridity, resembling that of the savannas of modern Africa. The term that best describes this climate is temperate savanna. No similar climate is known in the modern world, at least over a large region.

Community Ecology

Evidence indicates that Moss Acres Racetrack originally formed a permanent pond or lake situated in a savanna (defined as a landscape with a heterogenous mixture of open grassland and woodlands, with the woodlands rarely forming a dense canopy). The relative proportion of grassland to woodland in the area is unknown, though analogy with similar permanent water sources in modern African savannas and the abundance of browsers such as Amebelodon in the fauna suggests that a woodland was present in the immediate vicinity of the site, and a major component of the regional landscape.

One of the strangest aspects of the Moss Acres Racetrack fauna is the virtual nonexistence of terrestrial carnivores, considering the abundance of potential herbivore prey at the locality. There are three possible explanations for this absence: 1) terrestrial carnivores were present in the fauna, but so rare that they were missed by simple random chance; 2) carnivores were present at the locality but not preserved in the fossil fauna due to taphonomic bias; and 3) carnivores were actually absent from the fauna. Of these hypotheses the first is most plausible, though there is no basis for eliminating the third hypothesis. The second hypothesis is highly implausible, and can be excluded from consideration.

Many (though not all) modern savannas in Africa are governed by a process called facilitation, involving a tight interrelationship between rainfall, migraory grazing ungulates, and grass. In facilitation, seasonal rainfall drives grass productivity (high in the wet season, low in the dry season), productivity that is secondarily modified by extensive ungulate grazing. Large ungulates like the wildebeest and zebra graze tall, nutritionally poor grass during the rainy season, stimulating the shortened grass to produce nutritious new growth that can be utilized by smaller ungulates like the Thomson's gazelle. This process occurs continuously throughout the wet season, resulting in a landscape that is heterogeneous in terms of grass height.

The question arose as to whether some version of facilitation might have been practiced by the grazing portion of the Moss Acres Racetrack fauna as a means of increasing the number of available niches, and thus supporting its high diversity. This question was investigated from a variety of perspectives, examined lines of evidence including muzzle morphology, body mass distribution, and digestive physiology. Unfortunately, no clear conclusion could be drawn from the available evidence either for or against facilitation. However, it was pointed out that substantial differences in climate between the late Miocene of North America and modern Africa make a close convergence between these two ecosystems unlikely considering the crucial role played by climate in the modern process of facilitation.

Modern elephants play a special ecological role in maintaining African savannas; they act as mobile disturbances, thinning and clearing woodlands locally and hindering the spread of the woodlands onto the grassland to create a heterogeneous habitat structure conducive to biotic diversity. There is clear evidence that Amebelodon and other gomphotheres damaged or destroyed trees like modern African elephants, and this finding implies that Amebelodon may have played a similar ecological role in maintaining North

American late Miocene savannas. The presence of Amebelodon in the fauna reinforces the plausibility of the hypothesis that a grassland/woodland mosaic existed in the vicinity of Moss Acres Racetrack.

Concluding Remarks

Because of the generally high quality and taxonomic diversity of its specimens, the existence of a significant palynoflora, and geological conditions that minimize the likkelihood of specimen transport, the Moss Acres Racetrack site and to a lesser extent the Withlacoochee River 4A site provide an unprecedented window into the early Hemphilian of southeastern North America. This body of evidence allows the overall biotic and climatic conditions at the site to be better evaluated than for just about any other Miocene site in Florida (its only plausible rivals are the Hemingfordian Thomas Farm and the Clarendonian Love sites), and for the late Miocene perhaps the entire Gulf Coastal Plain. The amount of paleontological information available for Moss Acres Racetrack is matched by some late Miocene Great Plains sites (e.g., the late Hemphillian Coffee Ranch of the Texas Panhandle), and detailed commparison of these faunas in future studies may increase knowledge about regional variation in conditions across North America during the late Miocene. In turn, this knowledge when placed in a historical context could improve understanding of the biotic and climatic evolution of North America during the Miocene.

APPENDIX 1. A LIST OF POST-CRANIAL ELEMENTS REFERRED TO *AMEBELODON* (*KONOBELODON*) *BRITTI* FROM THE MOSS ACRES RACETRACK SITE IN THE COLLECTION OF THE FLORIDA MUSEUM OF NATURAL HISTORY.

UF 69944: left and right intact pelves.

UF 69992 (partial associated manus): magnum, unciform, scaphoid, trapezoid, and metacarpals I, III, and V.

UF 69997 (partial associated skeleton): right scapula; left and right ulnae; left and distal right radii; left and right lunars; left and right trapezia; left and right magna; left and right pisiforms; left and right scaphoids; left and right unciforms; left (II, IV, and V) and right (II, III, and IV) metacarpals; left and right femora; left and right tibiae; right fibula; left and right astragali; left calcaneum; left navicular; left entocuneiform; left and right cuneiforms; left and right cuboids; and left (I, II, III, and IV) and right (I, III, and V) metatarsals.

UF 95419: head of humerus.

UF 95420: partial scapula; distal ulna.

UF 113350: left tibia.

UF 135804: rib.

UF 135805: rib.

APPENDIX 2. *PEDIOMERYX HEMPHILLENSIS* SPECIMENS FROM THE MOSS ACRES RACETRACK SITE IN THE COLLECTION OF THE FLORIDA MUSEUM OF NATURAL HISTORY.

UF 69945: associated skull and mandibles
UF 69946: associated hindlimb
UF 97266: associated hindlimb
UF 97267: mandible
UF 113565: incisor

APPENDIX 4. FISH, REPTILE, AND BIRD SPECIMENS FROM THE MOSS ACRES RACETRACK SITE IN THE COLLECTION OF THE FLORIDA MUSEUM OF NATURAL HISTORY.

Class Chondrichthyes
Order Squaliformes
Family Lamnidae
Carcharodon auriculatus
UF 95424: tooth.
Family Carcharinidae
Negaprion brevirostris
UF 104243: tooth.
Galeocerdo sp.
UF 104247: tooth.
Order Rajiformes
Family Myliobatidae
UF 95423: tooth plate; UF 115603: tooth plate.

Class Osteichthyes
four uncatalogued associations of unidentifiable bones
Family Lepisosteidae
Lepisosteus sp.
UF 95401: associated scales and vertebrae; UF 115561: scale; UF 115621: scale.

Class Reptilia
Order Chelonia
Family Trionychidae
Apalone cf. *ferox*
UF 69926: associated partial carapace and plastron
Family Emydidae

Pseudemys sp.
UF 69927: partial carapace, plastron, and post-cranial skeleton; UF 69928: associated carapace, plastron, and post-cranials; UF 69931: associated carapace, plastron, and post-cranials; UF 94528: associated carapace elements; UF 95415: isolated peripheral; UF 95426: nearly complete carapace and plastron; UF 104246: epiplastron; UF 115586: pleural; UF 115587: disarticulated carapace; UF 115588: bridge; UF 115589: neural; UF 115604: shell fragments and phalanges; UF 115623: peripheral; UF 115624: seven associated peripherals; UF 115625: associated peripherals; UF 115626: neural; UF 117303: two associated marginals; UF 117304: associated neural and peripheral; UF 135843: shell fragments; UF 135844: shell fragments; UF 135845: two shell fragments; UF 135846: miscellaneous shell fragments; UF 135847: possibly associated plastron and carapace elements; UF 135848: carapace fragments.

APPENDIX 3. *APHELOPS MUTILIS* SPECIMENS FROM THE MOSS ACRES RACETRACK SITE IN THE COLLECTION OF THE FLORIDA MUSEUM OF NATURAL HISTORY.

UF 69938: pisiform; UF 69940: 11 associated thoracic vertebrae; UF 69941: canine, male; UF 69943: juvenile skull, dP1-dP4, M1, M2 unerupted; UF 69944: associated skeleton, including skull and mandible, male; UF 69970: metatarsal II; UF 69971: metacarpal II; UF 69972: metatarsal II; UF 69976: associated forelimb; UF 69978: proximal end of femur; UF 69979: proximal end of radius; UF 69980: proximal end of humerus; UF 69981: distal end of femur; UF 69984: distal end of tibia; UF 69985: partial astragalus; UF 69996: juvenile mandibular symphysis, deciduous incisors; UF 90291: deciduous lower incisor; UF 90292: proximal end of femur; UF 90300: partial associated forelimb; UF 90539: proximal end of radius; UF 90540: lateral ungual phalanx; UF 93466: lower cheektooth; UF 93467: associated pes; UF 93468: mandible; UF 95403: associated right forelimb; UF 95416: proximal end of scapula; UF 95417: two associated thoracic vertebrae; UF 97264: radius; UF 97265: associated skull, mandibles, and partial post-cranial skeleton, dP1, P2,dp4, m1, m2, m3 unerupted; UF 103713: mandible, male; UF 103714: skull, female; UF 115553: associated sesamoids; UF 115554: partial juvenile vertebra; UF 115557: patella; UF 115560: juvenile distal epiphysis of radius; UF 115562: juvenile distal end of radius; UF 115584: juvenile thoracic vertebra; UF 115590: caudal vertebra; UF 115595: fibula; UF 115612: distal end of fibula; UF 115613: associated magnum, cuneiform, unciform, and metacarpal V; UF 115614: cuneiform; UF 115615: juvenile thoracic vertebra; UF 115616: cervical vertebra centrum; UF 115633: partial juvenile skull, dP1, P2, dP3, DP4, M1-M3; UF 115634: partial skull; UF 115635: juvenile mandible, di1, p2, p3, dp4, m1-m3; UF 115637: atlas vertebra; UF 115636: distal end of humerus; UF 115638: patella; UF 115639: scaphoid and cuneiform; UF 115640: partial nuchal crest; UF 115641: associated juvenile phalanges and sesamoid; UF 115642: partial zygomatic arch; UF 115643: p3 or p4; UF 116843: associated skull and mandibles, female; UF 116844: skull; UF 115845: partial skull; UF 117320: sesamoid; UF 118542: associated manus; UF 135803: associated mandibles, male; UF 135807: metapodial; UF 135809: partial associated manus; UF 135812: mandibles, probable male; UF 135114: astragalus; UF 135825: distal end of metapodial; UF 135827: associated sesamoids; UF 135828: associated pelves; UF 135829: distal end of metapodial; 135830: distal end of metapodial; UF 135833: femur; UF 135834: associated tibia and partial fibula; UF 135837: atlas, axis, and cervical vertebrae III-VI.*

*: isolated specimen

Trachemys sp.
UF 118539: partial skeleton.
UF 118541: partial associated carapace and plastron.

Family Cheloniidae
Geochelone sp.
UF 117302: hyoplastron.

Order Crocodylia
Family Crocodylidae
Alligator sp.
UF 69929: associated post-cranial skeleton; UF 69930: associated partial post-cranial skeleton; UF 90288: coprolite; UF 90289: two teeth; UF 95427: skull, mandibles, and partial associated skeleton; UF 95514: partial associated skeleton; UF 115561: coprolite; UF 115564: osteoderm; UF 115566: coprolite; UF 115567: three assciated teeth; UF 115571: coprolite; UF 115573: tooth; UF 115574: coprolite; 115575: coprolite; UF 115596: coprolite; UF 115597: coprolite; UF 115598: coprolite; UF 115599: coprolite; UF 115600: coprolite; UF 115602: tooth; UF 155605: associated vertebrae; UF 115606: cranial fragment; UF 115607: ostoderm; UF 115608: proximal femur; UF 115609: vertebra; UF 115611: coprolite; UF 115627: complete skull and mandibles; UF 115629: associated partial post-cranial skeleton; UF 117305: two associated osteoderms; UF 17306: four associated osteoderms; UF 117307: three associated vertebrae; UF 117308: three associated vertebrae; UF 117309: partial jugal; UF 117310: partial scapula; UF 117311: coprolite; UF 117312: cranial fragments; UF 117313: seven associated vertebrae; UF 117314: associated cranial elements; UF 117315: tooth; UF 117316: phalanx; UF 117317: phalanx; UF 117318: proximal partial femur; UF 117319: assorted osteoderms; UF 118538: partial skeleton; UF 135808: coprolite; UF 135816: coprolite; UF 135819: coprolite.@
@: associated specimen

Class Aves
Family Anatidae
UF 117301: partial coracoid

APPENDIX 5. MISCELLANEOUS MAMMAL SPECIMENS FROM THE MOSS ACRES RACETRACK SITE IN THE COLLECTION OF THE FLORIDA MUSEUM OF NATURAL HISTORY.

Order Carnivora
Family Canidae
Osteoborus orc
UF 69948: cuboid; UF 104244: associated metacarpals III, IV, and V.

Order Sirenia
UF 95425: rib fragment (reworked).

Order Artiodactyla
Family Tayassuidae
UF 116846: partial deciduous premolar.

Family Camelidae
Genus indeterminate
UF 69949: proximal end of proximal phalanx; UF 69950: proximal end of proximal phalanx; UF 90290: associated distal end of proximal phalanx, medial and distal phalanges; UF 90542: patella; UF 93463: patella; UF 90541: distal end of juvenile metapodial; UF 95418: associated distal end of metapodial, medial and distal phalanges; UF 97262: proximal end of metatarsal; UF 104242: astragalus; UF 104249: partial calcaneum; UF 115569: proximal end of metapodial.

Hemiauchenia sp.
UF 93464: cuneiform.

cf. *Aepycamelus*/*Megatylopus*
UF 115630: cervical vertebra.

Family Gelocidae
cf. *Pseudoceras*
UF 95402: distal end of tibia.

Family Antilocapridae
UF 116847: astragalus.

APPENDIX 6. HORSE (EQUIDAE) SPECIMENS FROM THE MOSS ACRES RACETRACK SITE IN THE COLLECTION OF THE FLORIDA MUSEUM OF NATURAL HISTORY.

Tribe and genus indeterminate
UF 69956: associated partial scapula, partial humerus, and partial radius; UF 69957: radius distal end; UF 69958: associated pes; UF 69959: proximal phalanx; UF 69960: partial calcaneum; UF 69961: humerus distal end; UF 69962: associated pes; UF 69963: partial post-cranial skeleton; UF 69965: associated partial hindlimb; UF 90280: radio-ulna distal end; UF 90281: proximal metacarpal II; UF 90282: lateral ungual phalanx; UF 90283: medial phalanx proximal end; UF 90284: magnum; UF 90285: acetabulum; UF 90286: acetabulum; UF 90293: associated thoracic vertebrae and ribs; UF 90294: partial associated pes; UF 90295: humerus distal end; UF 90296: tibia distal end; UF 90297: cervical vertebra; UF 92997: proximal phalanx; UF 92998: medial phalanx; UF 93459: humerus distal end; UF 93460: humerus distal end; UF 93461: calcaneum; UF 93465: pisiform; UF 95389: magnum; UF 95393: lateral metapodial distal end; UF 95398: metatarsal III proximal end; UF 95411: associated metacarpals II, III, and IV; UF 95412: navicular; UF 103762: magnum; UF 103763: partial distal metapodial; UF 103764: lateral metapodial; UF 103765: humerus distal end; UF 103766: proximal phalanx; UF 103767: proximal phalanx; UF 103768: proximal phalanx; UF 104241: associated partial forelimb; UF 104245: petrosal; UF 104248: femur distal end; UF 115551: occipital; UF 115552: posterior portion of skull with atlas and axis; UF 115555: humerus distal end; UF 115556: seven associated caudal vertebrae; UF 115558: scapula; UF 115563: astragalus; UF 115568: incisor; UF 115570: proximal portion of proximal phalanx; UF 115572: medial phalanx; UF 115580: scapula; UF 115581: scapula; UF 115583: associated caudal vertebrae; UF 115591: lateral medial phalanx; UF 115593: incisor; UF 115601: associated vertebra and ribs; UF 115617: petrosal; UF 115618: petrosal; UF 115619: medial phalanx; UF 116848: six associated cervical and thoracic vertebrae; UF 116849: two associated thoracic vertebrae; UF 116850: proximal phalanx; UF 118540: ball of femur; UF 135810: associated metapodials; UF 135815: lumbar vertebra; UF 135817: associated ribs, cervical vertebra, and ball of femur; UF 135818: associated forelimb and incisor; UF 135820: medial phalanx; UF 135821: lateral ungual phalanx; UF 135822: lateral ungual phalanx; UF 135823: lateral ungual phalanx; UF 135824: associated, articulated hindlimb; UF 135832: juvenile tibia.

Tribe Equini
Genus indeterminate
UF 69953: mandibular symphysis.

cf. *Astrohippus*
UF 97270: associated forelimb.
Dinohippus sp.
UF 69952: M2; UF 92995: associated juvenile dentition, upper and lower; UF 95399: juvenile skull.

Calippus sp.
UF 65249: dP3 or dP4; UF 90287: partial lower molar; UF 90900: juvenile mandible.

Calippus mccartyi
UF 65249: dP3 or dP4; UF 69951: associated partial skull and mandible; UF 90287: m1 or m2; UF 90298: three associated lower toth fragments; UF 90299: P3 or P4; UF 95397: P3 or P4; UF 95407: P2; UF 95408: associated P3 and P4; UF 97275: p3 or p4.

Tribe Hipparionini
Hipparion cf. *tehonense*
UF 95388: m2; UF 95396: M3

Nannippus aztecus
UF 69933/69934: skeleton; UF 92994: P3 or P4; UF 39591: medial phalanx; UF 95392: thoracic vertebra; UF 95404: m1 or m2; UF 95409: associated m2 and m3; UF 95413: associated pes; UF 97263: associated right and left hindlimbs; UF 97271: P3 or P4; UF 97272: associated forelimb; UF 103755: lateral ungual phalanx; UF 103758: humerus distal end; UF 103759: thoracic vertebra; UF 103760: associated pes; UF 103857: medial phalanx; UF 138835: juvenile mandible; UF 135836: associated skull and mandibles; UF 135838: associated mandibles.

Nannippus morgani.
UF 95395: metatarsal; UF 97272: M1.

Cormohipparion sp.
UF 69966: partial skeleton; UF 69968: unworn upper molar.

Cormohipparion emslei
UF 95410: associated right M2 and left M2 and M3; UF 97259: associated mandibles; UF 97260: associated juvenile or fetal upper and lower dentition.

Cormohipparion plicatile
UF 69967: associated mandibles; UF 69968: M1 or M2; UF 93000: juvenile skeleton; UF 96306: associated M1-M2, left and right M3; UF 103754: associated mandibles.

Neohipparion trampasense
UF 65250: mandible; UF 69969: mandible; UF 135839: associated mandibles.

APPENDIX 7. LIST OF SPECIMENS RECOVERED FROM THE MOSS ACRES RACETRACK SITE DURING THE SPRING FIELD SEASON OF 1991, INCLUDING FIELD NUMBERS, DATE MEASURED, AND A DESCRIPTION OF SPECIMENS.

Field Number	Date Measured	Description
DL 1	April 11	_Amebelodon_ mandibular tusk
DL 2	May 1	_Amebelodon_ skull
DL 2*	April 11	separated upper tusk associated with DL 2
DL 3	April 13	_Amebelodon_ rib
DL 4	April 13	_Amebelodon_ mandible
DL 5	April 16	equid mandible
DL 6	April 16	associated miscellaneous ribs
DL 7	April 16	miscellaneous rib
DL 8	April 16	associated equid limb
DL 9	April 17	equid maxilla
DL 10	April 24	equid? scapula
DL 11	April 24	equid mandible
DL 12	April 24	associated equid metapodials
DL 13	April 24	associated equid skull and mandible
DL 14	April 24	_Aphelops_ mandible
DL 15	May 8	broken miscellaneous rib
DL 16	May 8	associated _Aphelops_ tibia and fibula
DL 17	May 14	miscellaneous rib
DL 18	May 14	miscellaneous rib
DL 19	May 14	equid skull
DL 20	May 14	_Aphelops_ femur
DL 21	May 14	miscellaneous rib
DL 22	May 15	associated _Aphelops_ radius and ulna
DL 23	May 15	miscellaneous rib
DL 24	May 15	equid? tibia
DL 25	May 21	unidentified long bone
DL 26	May 21	equid mandible
DL 27	May 29	_Amebelodon_ skull
DL 27*	May 22	upper tusks within the _Amebelodon_ skull DL 27
DL 28A	May 22	_Amebelodon_ pelvis
DL 28B	May 29	equid tibia

DL 29	May 29	associated *Aphelops* vertebrae
DL 30	May 30	*Amebelodon* skull
DL 31A	May 30	miscellaneous rib
DL 31B	May 30	*Aphelops* metapodial
DL 32	June 7	*Amebelodon*? rib

APPENDIX 8. POSITIONAL AND ORIENTATIONAL DATA FOR SELECTED SPECIMENS COLLECTED FROM THE MOSS ACRES RACETRACK SITE DURING THE FIELD SEASON OF SPRING 1991.

Field #	Depth (cm)	Direction (deg. E of N)	Distance (cm)	Bearing (deg. E of N)	Supplementary angle of bearing (deg. if >180)	Plunge (deg.)
DL 1	-228	73	380	90		9
DL 2	-139	79	522	145		8
DL 3	-196	110	377			
DL 4	-224	105	350			
DL 5	-195	85	335	83	83	18
DL 6	-170	76	396			
DL 7	-283	63	261	345	165	15
DL 8	-216	103	328	118		11
DL 9	-211	79	453	354	174	35
DL 10	-200	77	468	350	170	27
DL 11	-119	74	479	110		17
DL 12	-166	86	455	10		21
DL 13	-250	74	400	11		26
DL 14	-243	77	443	91		21
DL 15	-175	90	490	310	150	3
DL 16	-176	79	498	30		23
DL 17	-219	87	495	142		15
DL 18	-224	75	495	345	165	32
DL 19	-231	76	503			
DL 20	-210	81	512	255	75	4
DL 21	-234	87	438	71		31
DL 22	-219	86	557	78		32
DL 23	-150	73	588	84		30
DL 24	-210	82	628	93		22
DL 25	-173	70	611	323	143	30
DL 26	-164	80	663	345	165	28
DL 27	-94	79	825			
DL 28A	-211	111	395			
DL 28B	-213	105	493	339	159	15
DL 29	-232	95	595			
DL 30	-105	75	895			
DL 31A	-176	85	770	126		10
DL 31B	-96	76	954	199	19	19
DL 32	-107	85	942	179		20

LITERATURE CITED

Akersten, William A., Theresa M. Foppe, and George T. Jefferson, 1988. New source of dietary data for extinct herbivores. *Quaternary Research* 30: 92-97.

Alexander, R. McNeil, 1989. *Dynamics of Dinosaurs and Other Extinct Giants*. Columbia University Press: New York.

Allen, Joel A., 1880. *History of the North American Pinnipeds*. Washington Govenment Printing Office: Washington D.C.

Anderson, Philip, 1965. *The Reptiles of Missouri*. University of Missouri Press: Columbia, MO.

Attenborough, David, 1990. *The Trials of Life*. Little, Brown, and Company: Boston.

Auffenberg, Walter, 1967. Fossil crocodilians of Florida. *The Plaster Jacket* 5: 1-6.

Barbour, Erwin H., 1927. Preliminary notice of a new proboscidean *Amebelodon fricki*, gen. et sp. nov. *Bulletin of the Nebraska State Museum* 1(13): 131-134.

Barbour, Erwin H., 1929. The mandibular tusks of *Amebelodon fricki*. *Bulletin of the Nebraska State Museum* 1(14): 135-138.

Barbour, Erwin H., 1930. *Amebelodon sinclairi*, sp. nov. *Bulletin of the Nebraska State Museum* 1(17): 155-158.

Barbour, Erwin H., and Claude W. Hibbard, 1941. A shovel-tusked mastodon, *Amebelodon fricki*, from Kansas. *Bulletin of the Nebraska State Museum* 2(4): 3546.

Barghoorn, E. S., 1951. Age and environment: a survey of North American Tertiary floras in relation to paleoecology. *Journal of Paleontology* 25(6): 736-744.

Battan, Lois J., 1979. *Fundamentals of Meteorology*. Prentice Hall, Inc.: Englewood Cliffs, NJ.

Becker, Jonathan J., 1985. Fossil herons (Aves, Ardeidae) of the late Miocene and late Pliocene of Florida. *Journal of Vertebrate Paleontology* 5(1): 24-31.

Begon, Michael, John L. Harper, and Colin R. Townsend, 1986. *Ecology: Individuals, Populations, and Communities*. Sinauer Associates, Inc.: Sunderland, MA.

Behrensmeyer, Anna K., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4(2): 150-162.

Behrensmeyer, Anna K., and Dorothy E. Dechant Boaz, 1980. The recent bones of Amboseli National Park, Kenya. In Beherensmeyer, A. K. and A. P. Hill (eds.), Fossils in the Making. University of Chicago Press: Chicago.

Behrensmeyer, Anna K., J. D. Damuth, William A. DiMichelle, Richard Potts, Hans-Dieter Sues, and Scott L. Wing, 1992. Terrestrial Ecosystems through Time. University of Chicago Press: Chicago.

Bennett, Debra K., 1977. Paleontology, paleoecology, and biostratigraphy of the Rhinoceros Hill fauna (Hemphillian, latest Miocene), and sedimentology of the enclosing Ogallala Formation, Ash Hollow member, Wallace County, Kansas. M. S. thesis, University of Kansas, Lawrence.

Berta, Analisa, and Gary S. Morgan, 1985. A new sea otter (Carnivora, Mustelidae) from the late Miocene and early Pliocene of North America. Journal of Paleontology 59(4): 809-819.

Bertram, Brian, 1979. Serengeti predators and their social systems. In Sinclair, A. R. E.,and M. Norton-Griffiths (eds.), Serengeti. University of Chicago Press: Chicago.

Bjork, P. R., 1978. The functional significance of a broken lower incisor of Amphicaenopus, an Oligocene rhinoceratid. Proceedings of the South Dakota Acadamy of Sciences 57: 163-167.

Bonner, W. Nigel, 1984. Eared seals. In Macdonald, David (ed.), The Encyclopedia of Mammals. Facts on File Publications: New York.

Bourliere, Francois, and Malcom Hadley, 1970. The ecology of tropical savannas. Annual Review of Ecology and Systematics 1: 125-152.

Brain, C. K., 1980. Some criteria for the recognition of bone collecting agencies in African caves. In Beherensmeyer, A. K. and A. P. Hill (eds.), Fossils in the Making. University of Chicago Press: Chicago.

Brooks, H. K., 1981. Geologic Map of Florida. Institute of Food and Agricultural Sciences, University of Florida: Gainesville, FL.

Cabrera, Angel, 1929. Una revision de los mastodontes Argentinos. Revista del Museo del la Plata 32: 51-144.
Carroll, Robert L., 1988. Vertebrate Paleontology and Evolution. W. H. Freeman and Co.: New York.

Christol, J. de, 1832. (untitled). Annales de Sciences et du Industrie du Midi de la France 1: 180-181.

Colbert, Edwin H., 1935. Siwalik mammals in the American Museum of Natural History. *Transactions of the American Philosophical Society* 26: 1-401.

Cook, Harold J., 1922. Two new bunomastodonts from Colorado. *Proceedings of the Colorado Museum of Natural History* 4(1): 2-15.

Cope, Edward D., 1873. On some new extinct Mammalia from the Tertiary of the Plains. *Paleontological Bulletin* 14: 1-2.

Cope, Edward D., 1893. A preliminary report on the vertebrate paleontology of the Llano Estacado. *Fourth Annual Report to the Texas Geological Survey*: 1-136.

Critchfield, Howard J., 1983. *General Climatology*. Prentice-Hall Inc.: Englewood Cliffs, NJ.

Dahlquest, William W., 1983. Mammals of the Coffee Ranch Local Fauna of Texas. *The Pearce-Sellards Series* 38: 1-41.

Dowsett, Harry J., Thomas M. Cronin, Richard Z. Poore, Robert S. Thompson, Robin C. Whatley, and Adrian M. Wood, 1992. Micropaleontological evidence for increased meridional heat transport in the North Atlantic Ocean during the Pliocene. *Science* 258: 1133-1135.

Dundee, Harold A., and Douglas Rossman, 1989. *The Amphibians and Reptiles of Louisianna*. The Louisianna State University Press: Baton Rouge.

Edwards, S. W., 1982. A new species of *Hipparion* (Mammalia, Equidae) from the Clarendonian (Miocene) of California. *Journal of Vertebrate Paleontology* 2(2): 173-183.

Efremov, J. A., 1940. Taphonomy: a new branch of paleontology. *Pan-American Geologist* 74: 81-93.

Eisenberg, John F., 1981. *The Mammalian Radiations*. The University of Chicago Press: Chicago.

Elderfield, H., 1986. Strontium isotope stratigraphy. *Paleogeography, Paleoclimatology, and Paleoecology* 57: 71-90.

Estes, James A., 1989. Adaptations for aquatic living carnivores. In Gittleman, John L. (ed.), *Carnivore Behavior, Ecology, and Evolution*. Comstock Publishing Associates of the Cornell University Press: Ithica, N.Y.

Frick, Childs, 1937. Horned ruminants of North America. *Bulletin of the American Museum of Natural History* 69: 1-669.

Gaziry, Abdel Wahid, 1987. Remains of Proboscidea from the early Pliocene of Sahabi, Libya. In Boaz, Hoel T., Ali El-Arnault, Abdel Wahid Gaziry, Jean de Heinzelin, and Dorothy Dechant Boaz (eds.), Neogene Paleontology and Geology of Sahabi. Alan R. Liss, Inc.: New York.

Gidley, J. W., 1903. A new three-toed horse. Bulletin of the American Museum of Natural History 19: 465-476.

Graham, A., 1964. Origin and evolution of the biota of southeastern North America: Evidence from the fossil plant record. Evolution 18: 571-583.

Gregory, Joseph T., 1945. An Amebeolodon jaw from the Texas Panhandle. University of Texas Publication 4401: 477-484.

Harrar, Ellwood S., and J. George Harrar, 1962. Guide to Southern Trees. Dover Publications, Inc.: New York.

Hendey, Q. B., 1978. Late Tertiary Mustelidae (Mammalia, Carnivora) from Langebaangweg, South Africa. Annals of the South African Museum 76(10): 329-357.

Hill, Andrew P., 1979. Disarticulation and scattering of mammal skeletons. Paleobiology 5(3): 261-274.

Hill, Andrew P., 1980. Early post-mortem damage to the remains of some contemporary East African mammals. In Beherensmeyer, A. K. and A. P. Hill (eds.), Fossils in the Making. University of Chicago Press: Chicago.

Hintze, J., 1987. Number Cruncher Statistical Analysis 5.01. Published by author.

Hirschfield, Sue, and S. David Webb, 1968. Plio-Pleistocene megalonychid sloths of North America. Bulletin of the Florida State Muesum 12(5): 213-296.

Hulbert, Richard C., 1982. Population dynamics of the three-toed horse Neohipparion from the late Miocene of Florida. Paleobiology 8(2): 159-167.

Hulbert, Richard C., 1987. Late Neogene Neohipparion and Hipparion (Mammalia, Equidae) from the Gulf Coastal Plain of Florida and Texas. Journal of Paleontology 61: 809-830.
Hulbert, Richard C., 1988a. Calippus and Protohippus (Mammalia, Perissodactyla, Equidae) from the Miocene (Barstovian-early Hemphillian) of the Gulf Coastal Plain. Bulletin of the Florida State Museum, Biological Sciences 32: 221-340.

Hulbert, Richard C., 1988b. A new Cormohipparion (Mammalia, Equidae) from the Pliocene (latest Hemphillian and Blancan) of the Gulf Coastal Plain. *Journal of Vertebrate Paleontology* 7(4): 451-468.

Hulbert, Richard C., 1988c. *Cormohipparion* and *Hipparion* (Mammalia, Perissodactyla, Equidae) from the late Neogene of Florida. *Bulletin of the Florida State Museum, Biological Sciences* 33: 229-338.

Hulbert, Richard C., 1992. A checklist of fossil vertebrates in Florida. *Papers in Florida Paleontology* 6: 1-35.

Hulbert, Richard C., 1993a. Taxonomic evolution in North American Neogene horses: the rise and fall of an adaptive radiation. *Paleobiology* 19(2): 216-234.

Hulbert, Richard. C., 1993b. Late Miocene *Nannippus* (Mammalia, Perissodactyla) from Florida, with a description of the smallest hipparionine horse. *Journal of Vertebrate Paleontology* 13(3): 350-366.

Hutchinson, G. E., 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *American Scientist* 93: 145-159.

Jackson, Robert D., 1977. The fossil fresh water emydid turtles of Florida. Ph. D. dissertation, University of Florida, Gainesville.

Janis, Christine M., 1986. Evolution of horns and related structures in hoofed mammals. *Discovery* 19(2): 8-17.

Janis, Christine M., 1990. Correlation of cranial and dental variables with body size in ungulates and macropodoids. In Damuth, John and Bruce MacFadden (eds.), *Body Size in Mammalian Paleobiology*. Cambridge University Press, Cambridge, U.K.

Janis, Christine M., and Ehrhardt, D., 1988. Correlation of relative muzzle width and relative incisor width with dietary preferences in ungulates. *Zoological Journal of the Linnaean Society* 92: 267-284.

Janis, Christine M. and Wilhelm, Patricia B., 1993. Were there pursuit predators in the Tertiary? Dances with wolf avatars. *Journal of Mammalian Evolution* 1(2): 103-125.

Jarman, P. J., 1974. The social organization of antelope in relation to their ecology. *Behavior* 48: 213-267.

Jarman, P. J., and A. R. E. Sinclair, 1979. Feeding strategy and patterns of resource-partitioning in ungulates. In Sinclair, A. R. E.,and M. Norton-Griffiths (eds.), *Serengeti*. University of Chicago Press: Chicago.

Kenyon, Karl. W., 1975. The Sea Otter in the Eastern Pacific Ocean. Dover Publications Inc.: New York.

Kingdon, Jonathan, 1971. East African Mammals. Academic Press: New York.

Krebs, Charles J., 1984. Voles and lemmings. In MacDonald, David (ed.), The Encyclopedia of Mammals. Facts on File Publications: New York.

Krebs, Charles J., 1987. Ecology: The Experimental Analysis of Distribution and Abundance. Harper and Row Publishers: New York.

Kurten, Bjorn, and Elaine Anderson, 1980. Pleistocene Mammals of North America. Columbia Press: New York.

Lambert, W. David, 1989. The morphology and ecology of feeding in the shovel-tusked gomphotheres (Proboscidea, Gomphotheriidae, Amebelodontinae). M.A. thesis, University of Florida, Gainesville.

Lambert, W. D., 1992. The feeding habits of the shovel-tusked gomphotheres: evidence from tusk wear patterns. Paleobiology 18: 132-147.

Laporte, Leo F., 1979. Ancient Environments. Prentice-Hall, Inc.: Englewood Cliffs, NJ.

Lawlor, Timothy E., 1979. Handbook to the Orders and Families of Living Mammals. Mad River Press: Eureka, CA.

Leidy, Joseph, 1855. A memoir on the extinct sloth tribe of North America. Smithsonian Contributions to Knowledge 7: 1-68.

Leidy, Joseph, 1886. Mastodon and llama from Florida. Proceedings of the Academy of Natural Sciences, Philadelphia 38: 11-12.

Leidy, Joseph, 1887. Fossil bones from Florida. Proceedings of the Academy of Natural Sciences, Philadelphia 39: 309-310.

Leite, Michael B., 1990. Stratigraphy and paleontology of the Ash Hollow Formation (upper Miocene) on the north shore of Lake McConaughy, Keith County, Nebraska. University of Wyoming Contributions to Geology 28(1): 1-30.

MacFadden, Bruce J., 1984. Systematics and phylogeny of Hipparion, Neohipparion, Nannippus, and Cormohipparion (Mammalia, Equidae) from the Miocene and Pliocene of the New World. Bulletin of the American Museum of Natural History 179(1): 1-196.

MacFadden, Bruce J, 1986. Late Hemphillian monodactyl horses (Mammalia, Equidae) from the Bone Valley Formation of central Florida. Journal of Paleontology 60(2): 466-475.

MacFadden, Bruce J., 1992. Fossil Horses: Systematics, Paleobiology, and Evolution of the Family Equidae. Cambridge University Press: New York.

MacFadden, Bruce J., and Richard H. Hulbert, 1990. Body size estimates and distribution of ungulate mammals from the late Miocene Love Bone Bed of Florida. In Damuth, John and Bruce MacFadden (eds.), Body Size in Mammalian Paleobiology. Cambridge University Press, Cambridge, U.K.

Maddock, Linda, 1979. The "migration" and grazing succession. In Sinclair, A. R. E.,and M. Norton-Griffiths (eds.), Serengeti. University of Chicago Press: Chicago.

Maiorana, Virginia C., 1990. Evolutionary strategies and body size in a guild of mammals. In Damuth, John and Bruce MacFadden (eds.), Body Size in Mammalian Paleobiology. Cambridge University Press, Cambridge, U.K.

Maglio, Vincent J., 1969. A shovel-tusked gomphothere from the Miocene of Kenya. Breviora Museum of Comparative Zoology 310: 1-10.

Mason, C. F., and S. M. Macdonald, 1986. Otters: Ecology and Conservation. Cambridge University Press: Cambridge, UK.

Matthew, W. D., 1924. Third contribution to the Snake Creek fauna. Bulletin of the American Museum of Natural History 50(2): 59-210.

Matthew, W. D., 1926. The evolution of the horse; a record and its interpretation. Quarterly Review of Biology 1: 139-185.

Matthew, W. D., 1932. A review of the rhinoceroses with a description of Aphelops material from the Pliocene of Texas. Bulletin of the University of California Department of Geological Science 20(12): 411-480.

Matthew, W. D., and R. A. Stirton, 1930. Equidae from the Pliocene of Texas. Bulletin of the University of California Department of Geological Science 19: 349-396.

McDonald, H. Gregory, 1977. Description of the osteology of the extinct gravigrade edentate, Megalonyx, with observations on its ontogeny, phylogeny, and functional anatomy. MA thesis, University of Florida, Gainesville.

Mebrate, Assefa, 1987. The long-jawed gomphotheres. Ph. D. dissertation, University of Kansas, Lawrence.

Mellett, J., 1974. Scatological origin of microvertebrate fossil accumulations. Science 185: 349-350.

Merrian, J. C., 1916. Mammalian remains from the Chanac Formation of the Tejon Hills, California. California University, Department of Geological Sciences Bulletin 10: 111-127.

Meylan, Peter, 1984. A history of fossil amphibians and reptiles in Florida. The Plaster Jacket 44: 5-28.

Meylan, Peter, 1987. The phylogenetic relationships of soft-shelled turtles (family Trionychidae). Bulletin of the American Museum of Natural History 186: 1-101.

Migdalski, Edward C., George S. Fichter, and Norman Weaver, 1983. Fresh and Salt Water Fishes of the World. Crown Publishers Inc.: New York.

Mooser, O., 1968. Fossil Equidae from the middle Pliocene of the Central Plateau of Mexico. The Southwestern Naturalist 13: 1-12.

Neal, Earnest G., 1977. Badgers. Blandford Press: Poole, UK.

Neal, Earnest G., 1986. The Natural History of Badgers. Facts on File Publications: New York.

Nowak, Ronald M. and John L. Paradiso, 1983. Walker's Mammals of the World. Johns-Hopkins University Press: Baltimore.

Olson, Everett C., 1952. The evolution of a Permian vertebrate chronofauna. Evolution 6: 181-196.

Osborn, Henry F., 1936. Proboscidea, Vol. I. The American Museum Press: New York.

Osborn, Henry F., and Walter Granger, 1931. The shovel-tuskers, Amebelodontinae, of Central Asia. American Museum Novitates 470: 1-12.

Owen-Smith, R. N., 1984. Rhinoceroses. In Macdonald, D. (ed.), The Encyclopedia of Mammals. Facts on File Publishers: New York.

Owen-Smith, R. N., 1988. Megaherbivores. Cambridge Press: Cambridge, U.K.

Peterson, Roger Tory and Margaret McKenny, 1968. Wildflowers: Northeastern/Northcentral North America. Houghton-Mifflin Co.: Boston.

Pilgrim, Guy Ellcock, 1931. Catalogue of the Pontian Carnivora of Europe. British Museum: London.

Pirkle, E. C., 1956. The Hawthorne and Alachua Formations of Alachua County, Florida. Quarterly Journal of the Florida Academy of Sciences 19(4): 197-240.

Pirkle, E. C., W. H. Yoho, and A. T. Allen, 1965. Hawthorne, Bone Valley, and Citronelle sediments of Florida. Quarterly Journal of the Florida Academy of Sciences 28(1): 7-58.

Pratt, Ann E., 1986. The taphonomy and paleoecology of the Thomas Farm Local Fauna (Miocene, Hemingfordian), Gilchrist County, Florida. Ph.D. dissertation, University of Florida, GAinesville.

Prothero, Donald R., and Paul C. Sereno, 1982. Allometry and paleoecology of medial Miocene dwarf rhinoceroses from the Texas Gulf Coastal Plain. Paleobiology 8(1): 16-30.

Puri, Harbans S. and Robert O. Vernon, 1964. Summary of the geology of Florida and a guidebook to the classic exposures. Florida Geological Survey Special Publication 5: 1-312.

Quinn, J. H., 1955. Miocene Equidae of the Texas Gulf Coastal Plain. University of Texas, Bureau of Economic Geology, Publication 5516: 1-102.

Raup, David M. and Steven M. Stanley, 1978. Principles of Paleontology. W. H. Freeman and Company: New York.

Ray, Clayton E., 1960. Trichechodon huxleyi (Mammalia, Odobebenidae) in the Pleistocene of the southeastern United States. Bulletin of the Museum of Comparative Zoology 122: 129-142.

Repenning, Charles A., 1976. Enhydra and Enhydriodon from the Pacific coast of North America. Journal of Research of the U.S. Geological Survey 4(3): 305-315.

Retallack, Greg. J., 1982. Paleopedological perspectives on the development of grasslands during the Tertiary. Third North American Paleontological Convention Proceedings 2: 417-421.

Romer, Alred Sherwood, 1966. Vertebrate Paleontology. The University of Chicago Press: Chicago.

Rose, Francis L. and W. G. Weaver, 1966. Two new species of Chrysemys (=Pseudemys) from the Florida Pliocene. Tulane Studies in Geology 5(1): 41-48.

Rosevear, D. R., 1974. The Carnivores of West Africa. British Museum: London.

Roth, V. Louse, 1990. Insular dwarf elephants: a case study in body mass estimation and ecological inference. In Damuth, John and Bruce MacFadden (eds.), Body Size in Mammalian Paleobiology. Cambridge University Press, Cambridge, U.K.

Sarmiento, Guillermo, 1984. The Ecology of Neotropical Savannas. Harvard University Press: Cambridge, MA.

Savage, R. J. G., 1957. The anatomy of Potamotherium an Oligocene lutrine. Proceedings of the Zoological Society of London.129 (2): 151-244.

Schultz, G. E. (ed.), 1977. Guidebook Field Conference on Late Cenozoic Biostratigraphy of the Texas Panhandle and adjacent Oklahoma, August 4-6, 1977. Special Publication of the Kilgore Research Center, Dept. of Geology and Anthropology 1.

Scott, Kathleen M. (1990). Post-cranial predictors of ungulates as predictors of body size. In Damuth, John and Bruce MacFadden (eds.), Body Size in Mammalian Paleobiology. Cambridge University Press, Cambridge, U.K.

Scott, Thomas, 1988. The lithostratigraphy of the Hawthorn Group (Miocene) of Florida. Florida Geological Survey Bulletin 59: 1-148.

Sellards, E. H., 1914. The relation between the Dunnellon Formation and the Alachua Clays of Florida. Florida Geological Survey Annual Report 6: 161-162.

Sellards, E. H., 1916. Fossil vertebrates from Florida. A new Miocene fauna, new Pliocene species, the Pleistocene fauna. Florida Geological Survey Annual Report 8: 77-119.

Shipman, P., 1992. Body size and broken bones: preliminary interpretations of proboscidean remains. In Fox, John W., Calvin B. Smith, and Kenneth T. Wilkins (eds.), Proboscidean and Paleoindian Interactions. Baylor University Press: Waco, TX.

Shotwell, J. Arnold, 1961. Late Tertiary biogeography of horses in the Northern Great Basin. Journal of Paleontology 35: 203-217.

Shotwell, J. Arnold, 1963. The Juntura Basin: studies in earth history and paleoecology. Transactions of the American Philosophical Society 53(1): 1-77.

Simpson, George Gaylord, 1980. Splendid Isolation. Yale University Press: New Haven, CT.

Sinclair, A. R. E., 1979a. Dynamics of the Serengeti Ecosystem. In Sinclair, A. R. E., and M. Norton-Griffiths (eds.), Serengeti. University of Chicago Press: Chicago.

Sinclair, A. R. E., 1979b. The Serengeti environment. In Sinclair, A. R. E., and M. Norton-Griffiths (eds.), *Serengeti*. University of Chicago Press: Chicago.

Sinclair, A. R. E., and M. Norton-Griffiths (eds.), 1979. *Serengeti*. University of Chicago Press: Chicago.

Skinner, Morris and Walker Johnson, 1984. Tertiary stratigraphy and the Frick collection of fossil vertebrates from north-central Nebraska. *Bulletin of the American Museum of Natural History* 178(3): 215-358.

Skinner, Morris and Bruce J. MacFadden, 1977. *Cormohipparion* n. gen. (Mammalia, Equidae) from the North American Miocene (Barstovian-Clarendonian). *Journal of Paleontology* 51: 912-926.

Smithers, Reay H. N., 1983. *The Mammals of the Subsaharan African Subregion*. University of Pretoria: Pretoria, South Africa.

Stirton, R. A., 1936. A new ruminant from the from the Hemphill middle Pliocene of Texas. *Journal of Paleontology* 10: 644-647.

Stirton, R. A., 1940. Phylogeny of North American Equidae. *California University, Department of Geological Sciences Bulletin* 25: 165-198.

Stirton, R. A., 1944. Comments on the the relationships of the cervoid family Paleomerycidae. *American Journal of Science* 242: 644-647.

Stock, Charles, 1925. Cenozoic gravigrade edentates of western North America. *Publication of the Carnegie Institute of Washington* 331: 1-206.

Tanner, Lloyd G., 1967. A new species of rhinoceros, *Aphelops kimballensis*, from the latest Pliocene of Nebraska. *Bulletin of the Nebraska State Museum* 6(1): 1-16.

Tarasoff, F. J., A. Bisaillon, J. Pierard, and A. Whit, 1972. Locomotory patterns and external morphology of the river otter, sea otter, and harbor seal. *Canadian Journal of Zoology* 51: 915-927.

Taylor, Mark E., 1989. Locomotor adaptations by carnivores. In Gittleman, John L. (ed.), *Carnivore Behavior, Ecology, and Evolution*. Comstock Publishing Associates of the Cornell University Press: Ithaca, N.Y.

Tedford, R. A., M. F. Skinner, R. W. Fields, J. M. Rensberger, D. P. Whistler, T. Galusha, B. E. Taylor, J. R. MacDonald, and S. David Webb, 1987. Faunal succession and biochronology of the Arikarrean through Hemphillian interval (late Oligocene-earliest Pliocene epochs) in North America.

In Woodburne, M. O. (ed.), Cenozoic Mammals of North America. University of California Press: Berkeley, CA.

Tobien, Heinz, 1972. Status of the genus Serridentinus Osborn 1923 (Proboscidea, Mammalia) and related forms. Mainzer Geowisschlaftliche Mittelungen 1: 143-191.

Tobien, Heinz, 1973. The structure of the mastodont molar (Proboscidea, Mammalia) Part 1: the bunodont pattern. Mainzer Geowisschlaftliche Mittelungen 2: 115-147.

Tobien, Heinz, 1986. Mastodonts (Proboscidea, Mammalia) from the late Neogene and early Pleistocene of the People's Republic of China. Mainzer Geowisschlaftliche Mittelungen 15: 119-181.

Van Valkenburgh, Blaire, 1990. Skeletal and dental predictors of body size in carnivores. In Damuth, John and Bruce MacFadden (eds.), Body Size in Mammalian Paleobiology. Cambridge University Press, Cambridge, U.K.

Vernon, Robert O., 1951. Geology of Citrus and Levy Counties, Florida. Florida Geological Survey Bulletin 33: 1-256.

Voorhies, Michael R., 1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. University of Wyoming Contributions to Geology, Special Paper 1: 1-69.

Warter, J. K., 1976. Late Pleistocene plant communities-evidence from the Rancho Labrea tar pits. California Native Plant Society 2: 32-39.

Weaver, W. G. and J. S. Robertson, 1967. A re-evaluation of the fossil turtles of the Chrysemys scripta group. Tulane Studies in Geology 5(2): 53-66.

Webb, Paul W., and Robert W. Blake, 1985. Swimming. In Hildebrand, Milton, Dennis M. Bramble, Karel F. Liem, and David B. Wake (eds.), Functional Vertebrate Morphology. Belknap Press of Harvard Press: Cambridge, MA.

Webb, S. David, 1969. Pliocene Canidae of Florida. Bulletin of the Florida Museum of Natural History, Biological Sciences 14: 273-308.

Webb, S. David, 1977. A history of savanna vertebrates in the New World. Part I: North America. Annual Review of Ecology and Systematics 8: 355-380.

Webb, S. David, 1978. A history of savanna vertebrates in the New World. Part II: South America and the Great Interchange. Annual Review of Ecology and Systematics 9: 393-426.

Webb, S. David, 1983a. A new species of Pediomeryx from the late Miocene of Florida, and its relationships within the subfamily Cranioceratinae (Ruminantia, Dromomerycidae). Journal of Mammalogy 64(2): 262-276.

Webb, S. David, 1983b. The rise and fall of the late Miocene ungulate fauna in North America. In Nitecki, M. H. (ed.), Coevolution. University of Chicago Press: Chicago.

Webb, S. David, 1984. Ten million years of mammal extinctions in North America. In Martin, P. S., and R. G. Klein, (eds.), Quaternary Extinctions: A Prehistoric Revolution. University of Arizona Press: Tucson.

Webb, S. David, 1985. Late Cenozoic mammal dispersals between the Americas. In Stehli, F. G., and S. D. Webb (eds.) The Great American Biotic Interchange. Plenum Press: New York.

Webb, S. David, 1989a. Osteology and relationships of Thinobadistes segnis, the first mylodont sloth in North America. Advances in Neotropical Mammalogy 1989: 469-532.

Webb, S. David, 1989b. The fourth dimension in North American terrestrial mammal communities. In Morris, D. W., Z. Abramsky, B. J. Fox, and M. R. Willig (eds.), Patterns in the Structure of Mammalian Communities. Special Museum Publication of Texas Tech University, Lubbock.

Webb, S. David, and D. B. Crissinger, 1983. Stratigraphy and vertebrate paleontology of the central and southern phosphate districts of Florida. Geological Society of America, Southeastern Section, Field Trip Guidebook, Central Florida Phosphate District: 28-72.

Webb, S. David, and Sue. E. Hirschfeld, 1968. Plio-Pleistocene megalonychid sloths of North America. Bulletin of the Florida State Museum 12(5): 213-296.

Webb, S. David, and Richard C. Hulbert, 1986. Systematics and evolution of Pseudhipparion (Mammalia, Equidae) from the late Neogene of the Gulf Coastal Plain and the Great Plains. Contributions to Geology, University of Wyoming, Special Paper 3: 237-272.

Webb, S. D., MacFadden B. J., and Baskin, J. A., 1981. Geology and paleontology of the Love Bone Bed from the late Miocene of Florida. American Journal of Science 281: 513-544.

Webb, S. D., G. S. Morgan, R. C. Hulbert, D. S. Jones, B. J. MacFadden, and P. A. Mueller, 1989. Geochronology of a rich early Pleistocene vertebrate fauna, Leisey Shell Pit, Tampa Bay, Florida. Quaternery Research 32: 96-110.

Weier, T. Elliot, C. Ralph Stocking, and Michael G. Barbour, 1974. Botany, an Introduction to Plant Biology. John Wiley and Sons: New York.

Whitaker, John O., Jr., 1980. The Audobon Society Field Guide to North American Mammals. Alfred A. Knopf: New York.

Wiley, E. O., 1981. Phylogenetics. John Wiley and Sons: New York.

Wolfe, Jack A., 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. American Scientist 66(6): 694-703.

Zomlefer, Wendy, 1986. Common Florida Angiosperm Families, Parts I and II. Biological Illustrations, Inc.: Gainesville, FL.

BIOGRAPHICAL SKETCH

(William) David Lambert was born to William D. and Barbara J. Lambert in Cincinnati, Ohio, on November 11, 1963. He lived in Cincinnati until 1972, moving to Port Charlotte, Florida, where he maintained a legal residence until 1993. David attended Charlotte High School and graduated in 1982. In fall of 1982 David entered the University of Chicago, from which he graduated with general honors with a B.A. in biological science in spring of 1986. In fall of 1986 David entered the graduate program of the Department of Zoology at the University of Florida as a Master of Science candidate. In 1987 he began a program of study in the autecology and functional morphology of the shovel-tusked gomphothere proboscideans under the guidance of Dr. S. David Webb, Curator of Fossil Mammals at the Florida Museum of Natural History. He became a member of the Society of Vertebrate Paleontology in 1987, and was nominated for and awarded membership in the scientific research society Sigma Xi in 1989. David was awarded a Master of Science degree in zoology by the Department of Zoology in spring of 1989, and immediately afterward entered the doctoral program of the Department of Zoology at the University of Florida, where he began a program of research on the fauna and paleoecology of the Moss Acres Racetrack site. David's research interests primarily lay in vertebrate paleobiology, particularly that of mammals. He has performed research on a variety of subjects, including the behavioral and physiological ecology of dinosaurs, the systematics and ecology of proboscideans with an emphasis on Tertiary gomphotheres, proboscidean ivory microstructure and its application to paleoanthropology, and with Dr. Crawford Holling studied the implications of body mass distributions in late Pleistocene and Recent mammal faunas for the structural evolution of North America across the Pleistocene/Holocene boundary and the terminal Pleistocene mammal extinctions.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

S. David Webb

S. David Webb, Chairman
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Bruce MacFadden

Bruce MacFadden
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John F. Eisenberg

John Eisenberg
Katharine Ordway Professor of
Ecosystem Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Ronald Wolff

Ronald Wolff
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

C. S. Holling

Crawford Holling
Arthur R. Marshall, Jr.,
Eminent Scholar of
Ecological Sciences

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Douglas Jones
Professor of Geology

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fullfilment of the requirements for the degree of Doctor of Philosphy.

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